

SPATIAL ECOLOGY OF ANDEAN BEARS (*Tremarctos ornatus*) IN PROTECTED AREAS
AND RURAL COMMUNITIES' INTERACTIONS AT THE CHINGAZA MASSIF,
COLOMBIA

by

Ivan Mauricio Vela Vargas

Copyright © Ivan Mauricio Vela Vargas 2023

A Dissertation Submitted to the Faculty of the

THE SCHOOL OF NATURAL RESOURCES AND THE ENVIRONMENT

In Partial Fulfillment of the Requirements

For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

2023

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Dissertation Committee, we certify that we have read the dissertation prepared by: **Ivan Mauricio Vela Vargas**
titled: **SPATIAL ECOLOGY OF ANDEAN BEARS (*Tremarctos ornatus*) IN PROTECTED AREAS AND RURAL COMMUNITIES' INTERACTIONS AT THE CHINGAZA MASSIF, COLOMBIA**

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.



John Koprowski

Date: Jun 28, 2023



Jose Soto

Date: Jun 30, 2023



José F. González-Maya

Date: Jun 29, 2023

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.



John Koprowski

Dissertation Committee Chair

School of Natural Resources and the Environment

Date: Jun 28, 2023

ACKNOWLEDGMENTS

After several years of research and gaining skills in Colombia by visiting rural communities, performing biological expeditions, and learning how to conduct science and translate it into decision making processes, I would like to express my most sincere appreciation to all the people, institutions and the United States of America and Colombian governments that allowed me to pursue my Ph.D. degree at the University of Arizona.

First, I want to express my most sincere gratitude to my main advisor Dr. John L. Koprowski, because during the time that I have work with him, I learned the highest scientific and ethical standards in performing conservation science, but that is not all, I had the opportunity to share my time with the most sincere, honest and patient person. Thank you John, for allowing me to join the Koprowski Conservation Research Laboratory, for investing your time and efforts to make me a better scientist and a better person. Having you as an example is an honor and I always will be proud to say, "I was mentored by John Koprowski." John, you always offered me all the tools available to pursue my Ph.D. degree. More than anything you offered your help and complete support during the most difficult moments during my time at the University of Arizona.

I want to thank all the Koprowski Conservation Research Laboratory members, a group of top scientists and loving people that I will never forget from my time in Tucson and their travels to Colombia. Thanks to Dr. Melissa Merrick and Vicki Greer for their continuous support. Thanks to Brian Blais, Stuart Wells, Dr. Kira Hefty, Colin Brocka, Allie Burnett, Neil Dutt, Chris Banotai, Dr. Marina Morandini, Jeff Dolphin and Dr. Maria Vittoria Mazzamuto and all the lab members that supported me during these years.

Thank you to COLCIENCIAS now MINCIENCIAS (Ministry of Science, Technology, and Innovation of Colombia) and the Colombia Fulbright Commission for their support during this stage of my life, this is a unique opportunity to show how Colombian researchers can have success around the world.

Thanks to The University of Arizona for allow me to be a Wildcat, to the College of Agriculture and Life Sciences for their support and belief in me. To the School of Natural Resources and the Environment, especially to Katie Hughes for her unconditional support and advice during all these years.

Thanks to The Arizona Center for Nature Conservation – Phoenix Zoo and Reid Zoo Park for their support of my research and allowing me to participate in different conservation activities in Arizona and Colombia.

My special thanks to Dr Jan Schipper and Dr. Beth Polidoro for opening their house to me and making me feel like a member of their home.

Thanks to Dr. Jose Fernando González-Maya, Dr. Craig Wissler and Dr. Jose Soto for taking their time to be part of my dissertation committee.

To all my family that gave me strength when difficult times passed and overcoming the distance to always support me, I love you all.

To Juan Camilo Rubiano, Fernando Alvarez, Giacomo Cremonesi for their help during fieldwork. Special thanks to Juan Camilo that after supporting me during fieldwork is now a colleague in WCS Colombia. To Sebastian González for his help and collaboration in the generation of cartography for the study.

Thanks to all the staff of Proyecto de Conservación de Aguas y Tierras / ProCAT Colombia-International, thanks to Dr. Diego Zárrate, Dr. Andrea Jara, Camilo Paredes, Catalina Moreno and Angela Hurtado for their continuous support. It is like my second family.

Special thanks to Dr. José Fernando González-Maya, for all his support as a friend, colleague and in the role of conservation researcher.

Thanks to all the staff of the Chingaza National Natural Park for their help and support during my research, to Juan Carlos Clavijo, Chief of the protected area, Oscar Raigozo, Julian Zamora, Fredy Avellaneda, Angela Parra, Luis Linares, the rangers of Chingaza protected area. Without their help I would not been able to achieve all the fieldwork and the first capture of an Andean bear inside a protected area in Colombia.

Thanks to the staff of the Wakatá Zoological Park for their support during the capture of an Andean bear in Chingaza National Natural Park, especially to Catalina Rodriguez and Leonardo Arias.

Thanks to Wildlife Conservation Society Colombia program for the support during my fieldwork, the trust for me to coordinate the Andean bear program and the opportunity of being part of such a wonderful institution.

To my friends that believed in me, thank you all.

To all the people that I do not mention, thank you for your support and belief in me.

DEDICATION

To my wife Lorena Andrea Marín Carvajal, who always supports me in everything, this is for you, we made it.

To my parents that always show me the best example of being an active member of the society.

To my children Elena and Jacobo

To my brother Andres that besides the distance always has been on by my side.

To my sister Natalia who always watches my back.

To my angels that always are looking for me wherever they are.

This work is dedicated to the Andean bears, ghosts of the Paramo and the most beautiful and difficult animals to study.

TABLE OF CONTENTS

LIST OF FIGURES	8
LIST OF TABLES	9
ABSTRACT.....	10
INTRODUCTION	12
EXECUTIVE SUMMARY OF THE PRESENT STUDY.....	16
BIBLIOGRAPHY.....	17
APENDIX 1.....	20
APPENDIX 2.....	80
APPENDIX 3.....	111
APPENDIX 4.....	119

LIST OF FIGURES

Figure 1. Chingaza Paramo Complex and Chingaza National Natural Park location.	14
Figure 2. Adult male <i>Tremarctos ornatus</i> in the Chingaza National Protected Area, Colombia, July 2016. Used with permission of the photographer, Luis Guillermo Linares-Romero.....	77
Figure 3. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of an adult female <i>Tremarctos ornatus</i> from Nariño, Colombia (FNMH [Field Museum of Natural History] 88488. Photo used with permission of the Field Museum of Natural History, Chicago, Illinois. Condylbasal length is 193 mm.	78
Figure 4. Distribution of <i>Tremarctos ornatus</i> based on Velez–Liendo and García-Rangel (2017).	79
Figure 5. Location of the study area for assessing Andean bear occupancy in the context of Chingaza National Park, Colombia.....	108
Figure 6. Response curves of Andean bear occupancy relative to covariate values. Bold lines represent posterior means and ribbons represent 95% Bayesian credible intervals. DT: Euclidean Distance to Towns (m). NDVI: Normalized Difference Vegetation Index range -1 to 1.....	109
Figure 7. Predicted occupancy probability for Andean bear at the Chingaza Massif, Colombia. A. Fixed effect model, B. Random effect model, C. Disparity shows difference between predicted occupancy of Andean bear from fixed and random effects models, red areas are similar predictions and green areas shows greater disparity between predictions.....	110
Figure 8. Home range of an individual of Andean bear (<i>Tremarctos ornatus</i>) captured at the Chingaza National Park, Colombia (Local Convex Hull method).	117
Figure 9. Home range of an individual of Andean bear (<i>Tremarctos ornatus</i>) captured at the Chingaza National Park, Colombia (MCP method).	118
Figure 10. Study area and interviews performed at the Chingaza Massif, Colombia.....	142
Figure 11. Correspondence analysis for attitudes towards Andean bear at the Chingaza Massif, Colombia.....	143

LIST OF TABLES

Table 1. Model selection for occupancy of Andean bear at the Chingaza Massif, Colombia. The top 5 models were ranked with the expected predictive accuracy predictor (elpd). Δelpd represents the differences in elpd. ΔSE is the standard error of Δelpd and weight of each variable influencing the parameter of the models. Andean bear Occupancy (ψ) and detectability (p) parameters are indicated.	105
Table 2. Fixed effects model for Andean bear occupancy in the Chingaza Massif. DI: Euclidean Distance to human infrastructures, NDVI: Normalized Difference Vegetation Index, DT: Euclidean Distance to Towns.....	106
Table 3. Random Effects model for occupancy of Andean bear at the Chingaza Massif, Colombia. Variables used were DI: Euclidean Distance to human infrastructures (m), NDVI: Normalized Difference Vegetation Index, DT: Euclidean Distance to Towns.	107
Table 4. Attributes and levels used to create the hypothetical scenarios.	144
Table 5. Ranking of the generalized linear models ($\Delta\text{AIC} < 2$) and average model for the evaluation of Human-Andean Bear Conflict (HABC) on the Chingaza Massif, Colombia.	145
Table 6. Ranking of the generalized linear models ($\Delta\text{AIC} < 2$) and average model for the evaluation of Human-Andean Bear perceptions towards Andean bear on the Chingaza Massif, Colombia.....	146
Table 7. Random effects model estimation for Willingness to Accept (WTA) at the Chingaza Massif, Colombia.....	147

ABSTRACT

The main objective of this dissertation is to use evidence-based information to fill the gaps of knowledge of Andean bear (*Tremarctos ornatus*: Ursidae) in Colombia in order to understand the spatial ecology, interactions with human communities and to guide effective conservation programs for the species in Colombia. The National Conservation and Management Plan for the species in Colombia is outdated and failed to generate effective conservation measures, and lack of research of the species in Colombia resulted in the use of extrapolated information from other countries.

Andean bear is classified as Vulnerable (VU) to extinction by the International Union for the Conservation of Nature (IUCN) and the Colombian government. I first reviewed all the available published information of the species since its first description in order to identify knowledge gaps and to update the published information for the species across the global distribution.

With the knowledge of population dynamics, spatial ecology and interactions with human communities, I evaluated how landscape and anthropogenic variables affects occupancy patterns of the species at the Chingaza Massif and Chingaza National Park, located in the eastern range of Colombia and one of the main conservation cores of the species. During the fieldwork of this dissertation, the COVID-19 pandemic led to the mandatory lockdowns around the globe. With this opportunity we evaluated the effects of the “anthropause” during COVID-19 lockdowns performed by the Colombian government between March and August of 2020. Results showed that availability of natural habitats and human landscape variables affected the occupancy of the species at the Chingaza Massif of Colombia, and we reported for the first time the effects of COVID-19 pandemic in the occupancy rates of the species, showing that human activities affected significantly how Andean use landscapes at the Chingaza Massif.

In an effort to understand home range of the species at the Massif and in Colombia, one GPS satellite telemetry collar was installed in a wild individual, being the first Andean bear collared inside of a protected area in Colombia. The home range of the individual showed smaller home ranges (95% 140 km²; 50% 13km²) that the reported home ranges in South America.

In order to generate tools for management and conservation of Andean bears in Colombia, information about bear-human interactions, perceptions towards the species and the magnitude of negative interactions must be measured. This study took into account socio-economic and biological variables that described and evaluated the magnitude of human – Andean bear conflicts at the Chingaza Massif. Results showed that the main trigger of negative interactions is the lack of surveillance of domestic animals, and that rural ranchers prefer to be involved in conservation programs that maintain natural areas rather than simply being compensated for the livestock loss due to negative interactions. Evaluation of perceptions of rural communities regarding the presence of wildlife, particularly large carnivores such as Andean bears, is an essential input when generating mitigation and prevention tools for conflict events.

My study reports occupancy patterns of the species at the Chingaza Massif and the effects of how human activities affects how the species responds to human modified landscapes, in addition in a collaborative effort I was able to report for the first time the home range for the species in a protected area in Colombia. Including biological and socio-economic information about interaction dynamics between humans and Andean bears contributes to the generation of tools and methods to implement effective conservation strategies in areas where human communities and Andean bears overlap in adjacent areas of protected areas in Colombia.

The information generated during this research is replicable in any regional context in order to provide a strong methodological framework to study Andean bears to contribute to creation of conservation and interactions management plans.

INTRODUCTION

Andean bears (*Tremarctos ornatus*) are endemic to the tropical Andes and are South America's only bear species (Vela-Vargas *et al.*, 2021a). The Andean bear is listed as Vulnerable (VU) globally according with the International Union for Conservation of Nature's Red List (Velez-Liendo and Garcia-Rangel, 2017a) and nationally according with the Colombian government Resolution 1912 of 2017 (Ministerio de Ambiente y Desarrollo Sostenible, 2017). Despite being one of the most charismatic species in South America and considered as an umbrella species and an ecological model for protected areas management (Aconcha-Abril *et al.*, 2021; Crespo-Gascón and Guerrero-Casado, 2019; Garshelis, 2011; Parques Nacionales Naturales de Colombia and Wildlife Conservation Society, 2018), many aspects of its biology and conservation status are understudied or unknown (Kattan *et al.*, 2004; Peyton, 1999; Vela-Vargas *et al.*, 2021a). Lack of information presents an obstacle for long-term conservation initiatives, and particularly in Colombia, knowledge about the species is incipient and scarce, related mostly to distribution records (Cáceres-Martínez *et al.*, 2020a; Rodríguez *et al.*, 2019; Vela-Vargas *et al.*, 2014), human – Andean bear interactions (Escobar-Lasso *et al.*, 2020; Jorgenson and Sandoval, 2005; Parra-Romero *et al.*, 2019), diet (Cáceres-Martínez *et al.*, 2020b; Pisso-Florez *et al.*, 2021) and more recently genetic structure (Ruiz-García *et al.*, 2020a, 2020b). Therefore, prior management and conservation plans implemented in the country by the government have had limited effect (Rodríguez-Castro *et al.*, 2015).

Andean bears are distributed through the tropical Andes region at elevational ranges between 250 to 4250 m (Peyton, 1999; Vela-Vargas *et al.*, 2021a). In Colombia the species has been reported along the Andean Mountain ranges with a distribution that covers approximately 25% of the country, but that have been transformed due to the fact that 70% of the Colombian population inhabits this region (Armenteras *et al.*, 2011). Andean forest and Highland Paramos currently occupy less than 50% of their original distribution in Colombia (Llambí *et al.*, 2019). Andean bear suitable habitat has been reduced to 15% between 1970 and 2015 in Colombia (Cruz-Rodríguez *et al.*, 2020).

Habitat loss and fragmentation in mid to high elevations along the Andes range remain the primary threats to the species persistence. Additionally, the increased frequency of negative

human–Andean bear interactions has led to higher levels of mortality due to illegal hunting (Jorgenson and Sandoval, 2005; Kattan *et al.*, 2004; Parra-Romero *et al.*, 2019; Rojas-VeraPinto *et al.*, 2022).

Andean bears (*Tremarctos ornatus*) and human communities have long cohabited in the tropical Andean region of South America. As human density increases and space use by local communities expand, overall human and Andean bear interactions increase, and when interactions are negative at any level, human – Andean bear conflicts (HABC) arise and have also increased over time (Jorgenson, Sandoval, 2005, Goldstein *et al.*, 2006 Andrade *et al.*, 2019). The increase in the frequency and severity of HABC is considered as the second main threat to the species survival (Goldstein *et al.*, 2006, Ministerio Del Medio Ambiente, 2001, Vela-Vargas *et al.*, 2021, Velez–Liendo, Garcia-Rangel, 2017).

In Colombia, the peace agreement signed between the government and the Revolutionary Armed Forces of Colombia (FARC) guerrillas presented new opportunities for displaced communities to return to rural areas, generating new negative interactions between human – Andean bears in war-torn areas previously unoccupied by humans.

Human economies are affected by the loss of stock or crops and people are prone to invest in poor conflict management strategies misguided by anecdotal knowledge (Goldstein *et al.*, 2006b; Marchini, 2014; Sánchez-Mercado *et al.*, 2008). These dynamics are the consequence of productive human activities such livestock and agriculture in high elevation ecosystems, producing changes in habitat availability for Andean bears (Armenteras *et al.*, 2003; Kattan *et al.*, 2004), resulting in increased negative interactions that often lead to retaliatory killings of bears (Figueroa, 2015; Gárrido Corredor *et al.*, 2021; Sánchez-Mercado *et al.*, 2008)

One of the core areas for Andean bear conservation in Colombia is the Chingaza Massif, located within the eastern Andean range including Chingaza National Natural Park (Ch-NNP) (González-Maya *et al.*, 2017; Jorgenson and Sandoval, 2005) (Figure 1). This high-altitude complex is not only crucial for the conservation of Andean bears, but the Massif is also the principal source of water for Bogotá, the largest city and economic center of Colombia, providing 80% of the water consumed by its metropolitan area (Parques Nacionales Naturales de Colombia, 2016).

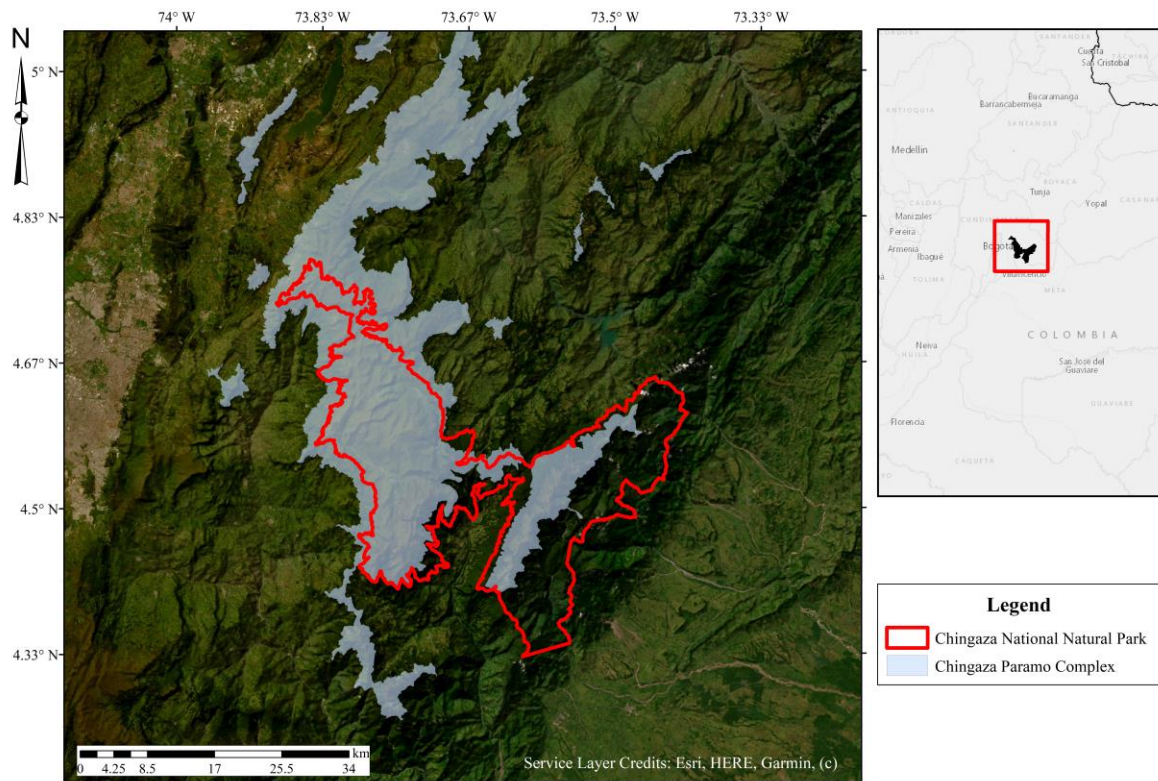


Figure 1. Chingaza Paramo Complex and Chingaza National Natural Park location.

Before the start of any conservation program, is a priority to know all the scientific information of any species in order to generate adequate management and conservation actions. Is because this I reviewed all the known published information of the species in South America for understand its ecology, behaviors and HABC interactions of Andean bear, and after this review a started to design and implement my research at the Chingaza Massif of Colombia.

In the constant search of balance between conservation of a umbrella species such the Andean bear and the improving of wellbeing of human communities that are in constant interaction with the species, I collected and analyzed biological and socio-economic information about Andean bears movements and interactions with rural communities in an integrative way to evaluate and propose methods to generate sustainable and realistic conservation plans for Andean bears and to seek sustainable practices to perform livestock and agriculture activities at the Chingaza Massif of Colombia. I highlight how Andean bears perceive and move on natural and productive landscapes and the effects of different human alterations that affects its presence at Chingaza National Natural Park and its buffer area.

My project was performed under the COVID-19 pandemic, which included mandatory lockdowns in Colombia and all over the world, presenting a unique chance to evaluate how the Andean bear occupancy rates changed having a landscape without humans constantly moving along the Massif, generating the first data about COVID-19 effects on Andean bear populations along its global distribution.

Understanding occupancy patterns is crucial to generate conservation actions, but in a collaborative effort with different organizations I was able to capture for the first time in Colombia an Andean bear inside of a protected area, and I reported the home range of Andean bear at the Chingaza National Natural Park.

Not only understanding the occupancy patterns of the species is important for its conservation, in order to generate and implement successful management actions for the species, is crucial the evaluation of the magnitude and perception of negative interactions that the species presents with human communities and the triggers that exasperate these dynamics, along this region of Colombia, and the potential solutions that could be applied in order to improve co-existence between human communities and Andean bears.

All the collected information allowed to understand and fill the gap of knowledge of Andean bear in Colombia and offers to stakeholders and decision makers ecological and socio-economic information of the species in order to generate and start conservation programs. Generation of hypothetical scenarios for the development of programs for management and mitigation of Human – Andean bear conflicts gives the opportunity of executing programs including technical support and traditional knowledge of rural communities. All the methods, and analyses discussed in this dissertation can be replicable for the development of conservation and protection programs and strategies for one of the most iconic species of South the Andean bear.

EXECUTIVE SUMMARY OF THE PRESENT STUDY

This research includes four manuscripts. The first manuscript published in *Mammalian species* (Appendix 1), “*Tremarctos ornatus* (Carnivora:Ursidae)”, which is and systematic review of all the published information of the species across its global range. The review showed that despite its charisma as an umbrella species, information of the Andean bear in South America refers to distributional records mostly, evaluation of its diet and interactions with human communities, but research about population dynamics, connectivity corridors and priority area for conservation still is scarce along South America and particularly in Colombia. Research on home ranges and population dynamics of the species is performed more in Ecuador and Perú, while research about distribution modelling have been performed with more regularity in Bolivia.

The second manuscript, intended for submission to *Hystrix* (Appendix 2) entitled “When humans are gone: Andean bear occupancy patterns and COVID-19 lockdowns effects at the Chingaza Massif, Colombia” evaluated occupancy patterns of the species at the Chingaza Massif of Colombia and the effects of COVID-19 mandatory lockdowns performed by the Colombian government during the pandemic. We identified the natural landscape covariables and anthropic variables affected occupancy patterns of Andean bears along the massif and how the effects of not having tourism and other activities along the massif increased the occupancy rates of the species.

The third manuscript published in *International Bear News*, entitled “Novel insights into Andean bear home range in the Chingaza Massif, Colombia”, described for the first-time the home range of the species at the Chingaza National Natural Park. The data analyzed in this manuscript provided information about how one individual moved along the protected area and showed the challenges of capturing Andean bears in Colombia.

The fourth manuscript, submitted for consideration in *Biological Conservation*, entitled “*Perception precedes reality? Interactions and opportunities for Andean bear conservation in the eastern range of Colombia*” characterized Human – Andean bear conflict triggers, assessed perceptions and evaluated the willingness to accept hypothetical conservation scenarios for Andean bears at the Chingaza Massif of Colombia.

BIBLIOGRAPHY

- Aconcha-Abril, I., Diaz, M., Marqu ez, R., Goldstein, I. 2021. Propuesta de hoja de ruta e indicadores para la evaluaci n de la implementaci n de la “Estrategia para la Conservaci n del oso andino en Parques Nacionales Naturales de Colombia. *In situ* 5: 238–249.
- Andrade, M., Espinoza, G., Moncada, J. 2019. Percepci n de actores clave acerca del conflicto ser humano-oso en la parroquia Plaza Guti rrez,  ntag, Imbabura, Ecuador. *Mammalia aequatorialis* 1: 43–50.
- Armenteras, D., Gast, F., Villareal, H. 2003. Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biol Conserv* 113: 245–256. doi:10.1016/S0006-3207(02)00359-2.
- Armenteras, D., Rodr guez, N., Retana, J., Morales, M. 2011. Understanding deforestation in montane and lowland forests of the Colombian Andes. *Reg Environ Change* 11(3): 693–705. doi:10.1007/s10113-010-0200-y.
- C ceres-Mart nez, C.H., Rivera-Torres, C.Y., L pez-Orjuela, H.A., Zamora-Abrego, J.G., Gonz lez-Maya, J.F. 2020a. Viviendo en los Andes: registros notables de la distribuci n altitudinal del oso andino, *Tremarctos ornatus* (Ursidae) en Boyac , Colombia. *Arx Misc Zool* 18: 161–171. doi:10.32800/amz.2020.18.0161.
- C ceres-Mart nez, C.H., S nchez Montano, L.R., Acevedo, A.A., Gonz lez-Maya, J.F. 2020b. Diet of Andean bears in Tam  National Natural Park , Colombia. *Ursus* 31(e10): 1–11. doi:10.2192/URSUS-D-18-00006.1.
- Crespo-Gasc n, S., Guerrero-Casado, J. 2019. The role of the spectacled bear (*Tremarctos ornatus*) as an umbrella species for Andean ecoregions. *Wildlife Research* 46(2): 176–183. doi:10.1071/wr18056.
- Cruz-Rodr guez, C., Reyes, A., Parra-Romero, A., Caceres-Martinez, C.H., Rodriguez, D., Lizcano, D., Z rrate-Charry, D., Restrepo, H., G mez, I., Aconcha-Abril, I., Vela-Vargas, I.M., Gonz lez-Maya, J.F., Nova Leon, L., Olaya-Herrera, H., Reyes-Amaya, N., Pulido-Santacruz, P., Marquez, R., Noguera-Urbano, E. 2020. El oso andino. Impactos de las acciones humanas sobre su distribuci n. In: Moreno, L.A., Andrade, G.I., Didier, G., hernandez-Manrique, O.(Eds.) Biodiversidad 2020. Estado y tendencias de la biodiversidad continental de Colombia. . Instituto de Investigaci n de Recursos Biol gicos Alexander von Humboldt , Bogot , D.C. .
- Escobar-Lasso, S., Cepeda-Duque, J., Gil-Fernandez, M., Gonz lez-Maya, J.F. 2020. Is the banana ripe? - Andean bear-human conflict in a protected area of Colombia. *Human - Wildlife Interactions* 14(2): 1–17.
- Figueroa, J. 2015. Interacciones humano–oso andino *Tremarctos ornatus* en el Per : consumo de cultivos y depredaci n de ganado. *Therya* 6(1): 251–278. doi:10.12933/therya-15-251.
- G rrido Corredor, A.M., Cottyn, H., Mart nez-Medina, S., Wheatley, C., S nchez, A., Kirshner, J., Cowie, H., Touza-Montero, J., White, P.C.L. 2021. Oso , Osito   a Qu  Ven s? Andean Bear Conflict , Conservation , and Campesinos in the Colombian P ramos. *Sustainability* 13(104889): 1–18. doi:https://doi.org/10.3390/ su131910489.
- Garshelis, D.L. 2011. Andean bear density and abundance estimates — How reliable and useful are they? *Ursus* 22(1): 47–64. doi:10.2192/URSUS-D-10-00030.1.
- Goldstein, I., Paisley, S., Wallace, R., Jorgenson, J.P., Cuesta, F., Castellanos, A. 2006. Andean bear – livestock conflicts: a review. *Ursus* 17: 8–15. doi:10.2192/1537-6176(2006)17.

- González-Maya, J.F., Galindo-Tarazona, R., Urquijo-Collazos, M.M., Zárata-Vanegas, M., Parra-Romero, A. 2017. El Oso Andino en el Macizo de Chingaza. Bogotá, Colombia.
- Jorgenson, J.P., Sandoval, A.S. 2005. Andean bear management needs and interactions with humans in Colombia. *Ursus* 16: 108–116.
- Kattan, G., Hernández, O.L., Goldstein, I., Rojas, V., Murillo, O., Gómez, C., Restrepo, H., Cuesta, F. 2004. Range fragmentation in the spectacled bear *Tremarctos ornatus* in the northern Andes. *Oryx* 38(02): 155–163. doi:10.1017/S0030605304000298.
- Llambí, L.D., Becerra, M.T., Peralvo, M., Avella, A., Baruffol, M., Flores, L.J. 2019. Monitoring Biodiversity and Ecosystem Services in Colombia's High Andean Ecosystems: Toward an Integrated Strategy. *Mt Res Dev* 39(3): A8–A20. doi:10.1659/MRD-JOURNAL-D-19-00020.1.
- Marchini, S. 2014. Who's in Conflict with Whom? Human Dimensions of the Conflicts Involving Wildlife. In: Penteadó, M., Silva, W.R., Verdade, L.M.(Eds.) *Applied Ecology and Human Dimensions in Biological Conservation*. Springer, Berlin. 189–209.
- Ministerio de Ambiente y Desarrollo Sostenible. 2017. Resolución 1912 de 2017 'Por la cual se establece el listado de las especies silvestres amenazadas de la diversidad biológica continental y marino costera que se encuentran en el territorio nacional, y se dictan otras disposiciones'.
- Ministerio Del Medio Ambiente. 2001. Programa nacional para la conservación en Colombia del Oso Andino *Tremarctos ornatus*.: 28 p. Bogotá, Colombia.
- Parques Nacionales Naturales de Colombia. 2016. Reformulacion Participativa Del Plan De Manejo Parque Nacional Natural Chingaza. 273 p. Bogotá, Colombia.
- Parques Nacionales Naturales de Colombia, Wildlife Conservation Society. 2018. Estrategia para la conservación del oso andino en los Parques Nacionales Naturales de Colombia (2016-2031).: 31p. Bogotá D.C.
- Parra-Romero, A., Galindo-Tarazona, R., González-Maya, J.F., Vela-Vargas, I.M. 2019. Not eating alone: Andean bear time patterns and potential social scavenging behaviors. *Therya* 10(1): 49–53. doi:10.12933/therya-19-625.
- Peyton, B. 1999. Spectacled bear conservation action plan. In: Servheen, C., Herrero, S., Peyton, B.(Eds.) *Bears: status survey and conservation action plan*. 157–198.
- Pisso-Florez, G.A., Gómez-Lora, I., Vela-Vargas, I.M., Pizo, H., Bedoya Dorado, I., Ramírez-Chaves, H.E. 2021. What's on the menu? A presumed attack of Andean bear on a Mountain tapir at the Puracé National. *Neotropical Biology and Conservation* 16(1): 19–25. doi:10.3897/neotropical.16.e57140.
- Rodríguez, D., Reyes, A., Gallegos-Sánchez, S. 2019. Northernmost distribution of the Andean bear (*Tremarctos ornatus*) in South America, and fragmentation of its associated Andean forest and Paramo ecosystems. *Therya* 10(2): 161–170. doi:10.12933/therya-19-756.
- Rodríguez-Castro, D., Contento, S., Grajales, D., Rodríguez, D. 2015. Evaluación del estado de aplicación del Programa Nacional para la Conservación en Colombia del Oso Andino (*Tremarctos ornatus*). *Rev Biodivers Neotrop* 5(1): 36–46.
- Rojas-VeraPinto, R., Bautista, C., Selva, N. 2022. Living high and aty risk: predicting Andean bear occurrence and conflicts with humans in southeastern Peru. *Glob Ecol Conserv* 36: e02112. doi:10.1016/j.gecco.2022.e02112.
- Ruiz-García, M., Arias-Vásquez, J.Y., Castellanos, A., Kolter, L., Shostell, J.M. 2020a. Molecular evolution (mitochondrial and nuclear microsatellites) in the Andean bear (*Tremarctos ornatus*: Ursidae, Carnivora): How many ESUs are there? In: Ortega, J., Maldonado, J.E.(Eds.)

Conservation genetics in mammals: Integrative research using novel approaches. Springer International Publishing, New York. 164–194.

- Ruiz-García, M., Vásquez, J.Y.A., Restrepo, H., Cáceres-Martínez, C.H., Shostell, J.M. 2020b. The genetic structure of the spectacled bear (*Tremarctos ornatus*; Ursidae, Carnivora) in Colombia by means of mitochondrial and microsatellite markers. *J Mammal* 101(4): 1072–1090. doi:10.1093/jmammal/gyaa082.
- Sánchez-Mercado, A., Ferrer-Paris, J.R., Yereña, E., García-Rangel, S., Rodríguez-Clark, K.M. 2008. Factors affecting poaching risk to Vulnerable Andean bears *Tremarctos ornatus* in the Cordillera de Merida, Venezuela: space, parks and people. *Oryx* 42(3): 437–447. doi:10.1017/S0030605308006996.
- Vela-Vargas, I.M., González-Maya, J.F., Pineda-Guerrero, A., Zárrate-Charry, D. 2014. Primer registro confirmado de Oso Andino (*Tremarctos ornatus*: Ursidae) en la Serranía de San Lucas, Bolívar, Colombia. *Mammalogy Notes* 1(1): 11–12.
- Vela-Vargas, I.M., Jorgenson, J.P., González-Maya, J.F., Koprowski, J.L. 2021. *Tremarctos ornatus* (Carnivora: Ursidae). *Mammalian Species* 53(1006): 78–94. doi:10.1093/mspecies/seab008.
- Velez-Liendo, X., Garcia-Rangel, S. 2017a. *Tremarctos ornatus*.

APENDIX 1.

Tremarctos ornatus (Carnivora:Ursidae)

I. Mauricio Vela-Vargas, Jeffrey P. Jorgenson, José F. González-Maya and John L. Koprowski
(Published in Mammalian species DOI: 10.1093/mspecies/seab008)

Corresponding Author: I. Mauricio Vela-Vargas
1064 East Lowell St., Room N326, Tucson, AZ 85721, USA
Telephone 520-621-7255 (Office),
Email: imvelavargas@email.arizona.edu; mauricio.vela@gmail.com

Mammalian Species 53(1006): 000-000

***Tremarctos ornatus* (Carnivora: Ursidae)**

**I. MAURICIO VELA-VARGAS, JEFFREY P. JORGENSEN, JOSÉ F. GONZÁLEZ-MAYA, AND JOHN
L. KOPROWSKI**

*School of Natural Resources and the Environment, N335 Environment and Natural Resources 2,
University of Arizona, Tucson, AZ 85721, USA; imvelavargas@email.arizona.edu (IMV-V);*

*U.S. Fish and Wildlife Service, Division of Scientific Authority, 5275 Leesburg Pike, MS: IA,
Falls Church, VA 22041-3803, USA; Jeffrey.Jorgenson@fws.gov (JPJ)*

*Proyecto de Conservación de Aguas y Tierras, ProCAT Colombia/International, Carrera 11 #
96 -43, Of. 303, Bogotá, Colombia; jfgonzalezmaya@gmail.com (JFG-M)*

*Haub School of Environment and Natural Resources, 201 Bim Kendall House, Laramie, WY
82072, USA, jkoprows@uwyo.edu (JLK)*

Abstract: *Tremarctos ornatus* (F.G. Cuvier, 1825) is a tremarctine bear commonly known as the Andean bear. It is a medium-sized bear with black to dark red-brown pelage with dense, long, coarse fur; creamy white marks occur on the chin, neck, and chest, and often white to creamy marks occur on the face, around the muzzle, and eyes. It is distributed in the tropical Andes of Venezuela, Colombia, Ecuador, Perú, Bolivia, and Argentina in South America. *T. ornatus* is catalogued as “Vulnerable” (VU) by the International Union for Conservation of Nature and Natural Resources and is included in CITES Appendix I. Main threats include habitat loss and fragmentation, illegal killing, human-bear conflicts, and most likely climate change.

Key words: Andean bear, Andean cloud forest, Andes Cordillera, bear; *Páramo*, South America, spectacled bear

Resumen: *Tremarctos ornatus* (F.G. Cuvier, 1825) es un oso tremarctino, conocido comúnmente como oso andino. Es un oso de tamaño medio, con pelaje denso, largo y grueso, de color negro a rojizo-café. Tiene marcas de color blanco - crema en el cuello y pecho, en la cara, alrededor del hocico y los ojos. La especie se distribuye en los Andes tropicales de Venezuela, Colombia, Ecuador, Perú, Bolivia y el norte de Argentina en Sur América. *T. ornatus* está catalogado como “Vulnerable” (VU) por la Unión Internacional para la Conservación de la Naturaleza y los Recursos Naturales y está incluida en el Apéndice I de CITES. Sus principales amenazas incluyen la pérdida y fragmentación de hábitats, cacería ilegal, conflictos humano – oso andino y probablemente el cambio climático.

Palabras clave: Bosque de niebla, Cordillera de los Andes, oso, oso andino, oso de anteojos, *Páramo*, Sur América

Tremarctos Gervais, 1855

Ursus: Lesson, 1827:129. Part; not Linnaeus, 1758.

Tremarctos Gervais, 1855:20 Type species *Ursus ornatus* F. Cuvier, 1825, by monotypy.

Helarctos: Gray, 1864:698. Part; not Horsfield, 1825.

Nearctos Gray, 1873:182. Type species *Helarctos ornatus* (= *Ursus ornatus* F. Cuvier, 1825), by monotypy.

CONTEXT AND CONTENT. Order Carnivora, suborder Caniformia, family Ursidae, subfamily Tremarctinae

Tremarctos ornatus (F. G. Cuvier, 1825)

Spectacled Bear

Ursus ornatus F. G. Cuvier, 1825:57. Type locality “Cordillères du Chili,” restricted to “las montañas al Este de Trujillo, departamento de la Libertad, Perú,” by Cabrera (1957: 242)

Ursus frugilegus Tschudi, 1844:90. Type locality unknown; stated as Perú, probably near Lima by Allen (1942:396; see “Nomenclatural Notes”).

Ursus fructilegus Schinz, 1845:34. Type locality “In Peru.”

Helarctos ornatus Gray, 1864:698. Type locality “South America, Cordilleras.”

Ursus nasutus Sclater, 1868:72, Plate VIII. Type locality not given (description based on a purchased specimen); stated as Simitarra River, Upper Magdalena, Colombia by María (1924).

Nearctos ornatus: Gray, 1873:182. Name combination.

Tremarctos ornatus: Gill, 1874:15. First use of current name combination.

Tremarctos ornatus majori Thomas, 1902: 216. Type locality “Southern Ecuador, probably the province of Azuay.”

Ursus ornatus thomasi Hornaday, 1911:748. Type locality “Andes of southern Colombia.”

Tremarctos lasallei María, 1924:115. Type locality “región de Arauca,” Colombia.

CONTEXT AND CONTENT. Context as for genus. *Tremarctos ornatus* is considered monotypic (Kitchener 2010).

NOMENCLATURAL NOTES. The monophyletic origin of Ursidae with the giant panda (*Ailuropoda melanoleuca*) as a sister clade is widely accepted (Agnarsson et al. 2010). *Tremarctos ornatus* and its related fossil forms are placed in a separate subfamily, Tremarctinae or “short-faced” bears, but this taxonomic classification is not universally accepted (Thenius 1976; Wilson and Reeder 2005; Garshelis 2009). Five specific or subspecific names have been applied to *T. ornatus*, based on claw length, facial markings, and body proportions. Allen (1942) refers to *U. frugilegus*, Tschudi 1844:90, *U. ornatus thomasi* Hornaday 1911:748, and *T. lasallei* María 1924:115 as synonyms of *T. ornatus majori*. Allen believed *U. frugilegus* to be inseparable from the species described by Cuvier. In a review of the materials collected by J. Tschudi in Peru (1838-1942) it was concluded that Tschudi’s description of *U. frugilegus* was based on discussions with local hunters rather than an actual specimen (Serrano-Villavicencio et al. 2020). Tschudi made no reference to a collected specimen, only commenting that “due to the local climate, preserving skins of this species was a difficult task”; as of 2020 no type material had been located (Serrano-Villavicencio et al. 2020:916).

Because all geographical forms were described by different authors based only on physical variations, Cabrera (1957) assigned all geographical forms as inadmissible, referring all variations to *Tremarctos ornatus* Cuvier, 1825. *T. ornatus*, is treated as a monotypic species, although considerable phenotypic variation is present within the species (Krause et al. 2008; Agnarsson et al. 2010; Kitchener 2010).

The etymological origin of the generic name came from *Trema* (Greek meaning hole) and *arktos* (Greek meaning bear) and refers to an unusual hole in the humerus. The specific name,

ornatus (Latin meaning “dress”—Gotch 1979), refers to the light-colored patches of fur surrounding the eyes, muzzle, chest, and throat. These characters contrast with the black-colored fur, which in some cases creates the appearance of eyeglasses (also called spectacles), and serves as the basis for one of its common English names: spectacled bear (Pérez-Torres 2001), whereas the other common English name is Andean bear (Velez–Liendo and García-Rangel 2017).

In several Andean indigenous cultures, the species is known as “*Jukumari*,” which means bear (Paisley and Saunders 2010). In Quechua, the word *uku* means “hole,” so the word probably was used as the “bear with holes in the eyes” (Pérez-Torres 2001). Throughout its range, *T. ornatus* is known by other common names, such as Mashíramo, Oso Frontino, Oso Salvaje, Oso Real, Uí, Oso Careto, Iznachi, Manaba, Puca mate, and Ucucu (Mondolfi 1989; Goldstein 2002; Castellanos et al. 2016a).

DIAGNOSIS

Tremarctos ornatus (Fig. 1) is a medium-sized bear (head–body length 1,190–1,740 mm—Mondolfi 1980; Bininda-Emonds 1998) and is larger than the sun bear (*Helarctos malayanus*, head–body length 1,000–1,400 mm—Fitzgerald and Krausman 2002), but is similar in size to the American black bear (*Ursus americanus*, head–body length 1,430 – 1,570 mm—Lariviere 2001). *T. ornatus* has the shortest muzzle (9–129 mm) of all bear species and the shortest mean (\pm *SD*) skull length of any bear species (201 ± 6.45 mm) only comparable with the sun bear (213 ± 13.15 mm—Christiansen 2007; Stucchi and Figueroa 2013). Claws are short on front and rear feet (Peyton 1980, 1999; Garshelis 2009) in comparison with the sun bear that has strongly curved and pointed claws (Fitzgerald and Krausman 2002). The mandible of *T. ornatus*

has a unique trait not present in other ursid species: a deep fossa called the premasseteric fossa (Mondolfi 1983).

GENERAL CHARACTERS

Tremarctos ornatus is a medium-sized bear with rounded ears, a plantigrade stance, front limbs longer than the hindlimbs, non-retractable curved claws, and a short tail (Mondolfi 1971; Nowak 1999; Peyton 1999; Garshelis 2009; García-Rangel 2012). Pelage is black to dark red-brown with dense, long, and coarse fur (Mondolfi 1971; Garshelis 2009). Body coat color varies from black or blackish brown to blackish red (Mondolfi 1989; Nowak 1999; Garshelis 2009). Individual bears usually exhibit white, yellowish or creamy marks around the eyes that continue to the muzzle, cheeks, throat, neck, and chest (María 1924; Allen 1942; Garshelis 2009; García-Rangel 2012). These marks are highly variable across the geographic range, not only in color but also size, and can range from prominent to completely absent (Allen 1942; Mondolfi 1971; Garshelis 2009; Reyes et al. 2017), and they are the most distinctive phenotypic character for *T. ornatus*. When present, facial marks are more conspicuous in young, whereas in adults the facial marks can become thinner with age; they do not indicate family relationships between individuals. (Van Horn et al. 2014a, 2015).

As with all bears, *T. ornatus* is sexually dimorphic; adult females are 67% as large as males (Mondolfi 1989; Garshelis 2009; García-Rangel 2012). Furthermore, male skulls are larger than female skulls (skull length [mean \pm SD] males = 236.8 \pm 12.0 mm; females = 202.2 \pm 21.8 mm) and males have a well-developed lambdoid crest and a prominent sagittal crest that is absent or reduced in females (Fig. 2; Emslie 1995; Stucchi and Figueroa 2013).

Head–body length for *T. ornatus* varies between 1,100–2,200 mm (Bininda-Emonds 1998; Nowak 1999; Garshelis 2009; García-Rangel 2012). Mean external measurements (mm; \pm *SD*; *n*—Mondolfi 1971) for males from Venezuela were: total length (1,485 \pm 360; 2), tail length (100; 1), ear length (100; 1), and mean weight (91 \pm 68 kg; 2). Colombian males in the wild have a mean head–body length of (1,350 \pm 219; 3), tail length (733 \pm 20; 3), ear length (103 \pm 18; 3) and weight (105 \pm 60 kg; 3). Females have a mean head–body length (1,260 \pm 28; 2), tail length (80 \pm 14; 2), ear length (100; 1), and mean weight (37.5 \pm 2 kg; 2—Rodríguez et al. 2013). Head-body length from one adult male from Ecuador was 1,312 mm, tail length 150 mm, and ear length 64 mm. Head–body length from one juvenile female in Ecuador was 270 mm and ear length 52 mm (Tirira 2009). *T. ornatus* from Bolivia weighed 34 kg (male subadult) and 30 kg (“undersized” adult male), but no other measurements were reported (Paisley 2001). No information is available for *T. ornatus* in Peru, except that Peyton (1980) estimated weights between 20 and 120 kg.

Derived from the oldest fossil specimen and four modern *T. ornatus*, skull and mandible measurements from *T. ornatus* (mm; mean \pm *SD*; Stucchi et al. 2009) were: condylobasal length 223.16 \pm 14.02, median palatal length 103.2 \pm 7.9, palatal breadth at M2 41.28 \pm 2.72, breadth at the labial C (upper canine) alveoli 57.62 \pm 2.31, breadth at the lingual C alveoli 34.4 \pm 2.06, zygomatic breadth 159.82 \pm 6.9, frontal breadth 84.74 \pm 8.45, least breadth between the orbits 62.22 \pm 6.98, facial length 114.44 \pm 2.61, mandible length 164.54 \pm 6.66, height of the coronoid process 95.18 \pm 7.87, basal length of the coronoid process 48.65 \pm 6.64, height of the horizontal ramus at M2 35.58 \pm 1.53.

Tremarctos ornatus lacks a diastema, unlike the insectivorous (e.g., the sloth bear, *Melursus ursinus*) and carnivorous (e.g., the polar bear, *Ursus maritimus*) bears (Figueirido et al. 2009; Stucchi and Figueroa 2013). The dental formula is $i\ 3/3, c\ 1/1, p\ 4/4, m\ 2/3$, total 42— (Ramsay 2003; García-Rangel 2012) and includes the shortest incisors in the Ursidae. The canines are bladed and an extra lateral cusp, located between the trigonid and taloned, occurs on m1 (Emslie 1995; Sacco and Van Valkenburgh 2004; Stucchi and Figueroa 2013).

The humerus of *T. ornatus* can be recognized by the presence of a fistula situated above the internal epicondyle (Cabrera and Yepes 1940). Davis (1958) described the tarsal ligaments of *T. ornatus* in comparison with human tarsal ligaments, detailing that the tarsus of *T. ornatus* is more flexible but is a less stable structure than in humans. *T. ornatus* has an enlarged radial sesamoid called “false thumb,” a feature shared with the panda. The function of this thumb is still debated (Salesa et al. 2006).

DISTRIBUTION

Tremarctos ornatus is distributed in the South American tropical Andes region (Fig. 3) in an elevational range between 200 to 4,250 m (Peyton 1980, 1981, 1999; García-Rangel 2012). During the Pleistocene, the distributional range was larger (Stock 1950). Currently the distribution is an elongated and narrow range that is about 200–650 km wide and 4,600 km long (Peyton 1999; Kattan et al. 2004; García-Rangel 2012), including six countries: Venezuela, Colombia, Ecuador, Perú, Bolivia, and Argentina (Mondolfi 1989; Peyton 1999; Garshelis 2009; García-Rangel 2012; Cosse et al. 2014; Velez–Liendo and García-Rangel 2017). *T. ornatus* potentially occurs in Panama, but there are no records to support its presence (Allen 1942; Hershkovitz 1957; Mondolfi 1971, 1989; Goldstein et al. 2008).

In Venezuela, *T. ornatus* is widely distributed in the Andes in discontinuous forested mountain areas in the western portion of the country (Lara, Táchira, Mérida, Portuguesa, Zulia, and Trujillo States—Osgood 1911; Mondolfi 1971, 1989; Goldstein 1992; Bisbal 1993; Soriano et al. 1999; Sánchez-Mercado et al. 2014).

In Colombia, *T. ornatus* has been reported from three biogeographic regions (Caribbean, Andes, and Pacific) and 20 departments (Alberico et al. 2000; Jorgenson and Sandoval-A 2005; Solari et al. 2013; Vela-Vargas et al. 2014; Cáceres-Martínez et al. 2016; Rodríguez et al. 2019). In Ecuador, *T. ornatus* is distributed in the Sierra, High Amazon, and Andes regions, and is present in both ranges of the Andes and the Condor and Cucutú sub-ranges (Suarez 1988; Castellanos 2011; Zapata-Ríos and Branch 2016). In Peru, *T. ornatus* is found in all three ranges of the Andes, with 973 records of presence distributed in 17 departments on an elevation range between 400–3,692 m (Márquez and Pacheco 2010; Falconi 2019; Falconi et al. 2020). In addition to Andean forest and páramos, *T. ornatus* lives in dry and humid tropical areas of less than 1,000 m elevation (Figueroa 2012; Figueroa and Stucchi 2013; Filipczyková et al. 2016; Appleton et al. 2018).

In Bolivia, *T. ornatus* is known from four departments: La Paz, Santa Cruz, Chuquisaca Cochabamba, and Tarija (Salazar and Anderson 1990; Anderson 1997; Martínez et al. 2008; Albarracín et al. 2013). The southern distributional extent of *T. ornatus* is the southern portion of Tarija department in Bolivia, coinciding with the northwestern border of Argentina (Vargas and Azurduy 2006). Derived from 18 unconfirmed sightings in northwestern Argentina, del Moral and Bracho (2005) suggested the presence of *T. ornatus* in the country. After several years of debate (Del Moral and Bracho 2005, 2009; Rumiz et al. 2012), Cosse et al. (2014) confirmed its

presence in Jujuy and Salta provinces in northern Argentina using noninvasive samples (hair and feces) to generate genetic identification.

The potential presence of *T. ornatus* in Panama is based on a skull and traditional knowledge from indigenous communities (Herskovitz 1957). Later, field surveys at the Serranía de Pirre (along the border with Colombia) were unable to confirm the presence of *T. ornatus* in Panama (Goldstein et al. 2008).

FOSSIL RECORD

The earliest tremarctine bears are known from late Miocene fossils in North America (Tedford and Martin 2001). Four genera of tremarctines are currently recognized: *Plionarctos* (extinct, two species), *Arctodus* (extinct, two species), *Arctotherium* (extinct, five species) and *Tremarctos* with two species, including the only extant species, *T. ornatus* (Soibelzon et al. 2005, 2008; Mitchell et al. 2016). The most complete fossil specimen includes skull, mandible vertebrae, ribs, hind limbs, and forelimbs and the oldest record of *T. ornatus*, an adult male from Chaquil Cave, Amazonas department, Peru, dated $5,980 \pm 50$ radiocarbon years ago, is reported by Stucchi et al. (2009). Additional records are from two archeological sites in Colombia dated from 4,030 and 2,725 years ago, in Cundinamarca department (Urrego-Correal 1990), and one fossil record from Peru dated from 1,500 years ago in Cajamarca department (Florez 1975). These fossil records consist only of small pieces of bones (ulna, canine, metacarpus), but are the only specimens known. Skeletal remains from 700 BCE–250 CE were excavated at La Chimba site in Ecuador (Stahl and Athens 2001).

Tremarctine is considered monophyletic by Mitchell et al. (2016), but mtDNA phylogenetic analyses suggest that *Arctodus* (North America) and *Arctotherium* (South America)

lineages are not sister taxa (from a monophyletic clade), as suggested by Trajano and Ferrarezzi (1995). *Tremarctos* and *Arctotherium* are hypothesized to be sister taxa, diverging in the Pliocene. The estimated divergence estimation for *Arctodus* and *Tremarctos* is 5.66 million years ago (Krause et al. 2008). *Plionarctos* lineage is ancestral to *Arctodus*, *Arctotherium*, and *Tremarctos* but is constituted as a paraphyletic stem-group (Tedford and Martin 2001).

Based on three fossils of an ursine bear from the late Miocene in Nebraska (USA) described as *Aurorarctos tirawa* gen. et sp. nov. (two mandibles, 14 isolated teeth, and one partial humerus), Jiangzuo and Flynn (2020) hypothesized the monophyly of tremarctine bears, but the clade name Arctotheriini is used to represent the crown + stem group lineages. Tremarctinae is not eliminated but is just not used as a clade name because Jiangzuo and Flynn recognize Ursinae as the group containing not only the *Ursus* lineages (Ursini), but the tremarctines and the early ursine *Aurorarctos*.

FORM AND FUNCTION

Form.—The skull of *Tremarctos ornatus* is wide and heavy with thick boney walls and high bone density (Fig. 2; Christiansen 2008a; Stucchi and Figueroa 2013). These features could be a response to an omnivorous diet with high consumption of plants (Christiansen and Wroe 2007; Christiansen 2008b; Jiangzuo and Flynn 2020). *T. ornatus* possesses blade-shaped canines (bite force [mean \pm SD] at the canine tip = 607.52 \pm 143.77 N) with enlarged molars, characteristic traits of omnivorous species (Sacco and Van Valkenburgh 2004; Christiansen and Wroe 2007). The zygomaticomandibularis of *T. ornatus* is relatively larger than in other bear species showing a moderate bite force in comparison with specialized bears, such as the giant

panda (*Ailuropoda melanoleuca*—Davis 1955; Suárez 1985; Peyton 1999; Christiansen and Wroe 2007; García-Rangel 2012). In contrast, the superficial masseter is smaller than in other carnivores and differs from flesh-eating species in having a shorter, concave-shaped mandible that allows grinding and cutting movements (Davis 1955; Figueirido et al. 2009). These bone, teeth, and muscle characteristics are correlated with a predominantly herbivorous diet (Davis 1955; Christiansen and Wroe 2007; Figueirido et al. 2009; García-Rangel 2012). The tongue is wide (35 mm). The lips are large and flexible, as in all Ursidae (Davis 1955; García-Rangel 2012). Brain weight from a captive individual was 240 g (Hirata 1987).

In locomotion, *T. ornatus* uses only five ligaments in the talocrural articulation and a well-developed, inter-articular meniscus (14 mm long by 3 mm wide), which implies lateral thrust of the astragalus against the fibula in strong inversion, such as during climbing (Davis 1958). The radial sesamoid is medio-laterally flattened, whereas the distal tip is scarcely developed, like a blunt protuberance (Salesa et al. 2006).

Length of the baculum is 10.47 mm, height at the level of the basal end is 6.1 mm, height at the level of the distal end is 3.8 mm, and maximum width is 7.9 mm; these measurements were derived from one sub-adult male killed in Venezuela (Mondolfi 1983). The baculum is nearly straight, gradually tapered from base to tip, and ends in a slightly enlarged blunt tip (Mondolfi 1983).

The adaptive value of the large white marks on the muzzle, upper chest and neck, and the large white circles around the eyes is unknown; however, these regions might modulate intraspecific aggression and dominance (Caro 2009). All bears have epipharyngeal pouches. Based on the examination from one individual of *T. ornatus* (Forstenpointner and Weissengruber

2000), these are a single pouch and two smaller sacs that are outfoldings of the lateral pharyngeal wall. It is thought that these could play a role in the production of vocalizations via the movement of the neck and enable management of the air column (Forstenpointner and Weissengruber 2000; Weissengruber et al. 2001).

Ovaries in *Tremarctos ornatus* are located on the sublumbar region anterior of the kidneys (Enciso and Vásquez 2007). The mean length of the right ovary is 18.5 ± 2 mm ($n = 2$), 11.5 ± 2 mm width ($n = 2$), and 9 ± 1 mm thickness ($n = 2$). The mean length of the left is 19 mm ($n = 2$), width is 10.5 ± 2 mm ($n = 2$), and thickness is 8.5 ± 0.7 mm ($n = 2$ — Lengwinat et al. 2000; Enciso and Vásquez 2007). Macroscopically, the placenta (*Placenta discoidalis*) is disk-shaped with a length of 120 mm, width of 95 mm, thickness of 5 mm, and mass of 55.4 g (Michel et al. 1983).

Scrotum length and height are 465 and 629.5 mm, respectively. Testes are oval oblique to the dorsocaudal major axis (right testis 386 by 241.5 mm, left testis 476 by 241.5 mm—Sanchez-Arbouin and Nassar-Montoya 1997). Sperm measurements (mean \pm SD) were: head length 5.34 ± 0.15 μ m, head width 3.72 ± 0.05 μ m, area of head 16.84 ± 0.55 μ m², head perimeter 16.07 ± 0.32 μ m, acrosome 67.70 ± 3.38 %, area of intermedium piece 2.06 ± 0.22 μ m², and intermedium piece width 0.95 ± 0.09 μ m (Enciso et al. 2006). Sperm motility in males was recorded between 50–70%, with 10–15 % abnormalities (Sanchez-Arbouin and Nassar-Montoya 1997; Enciso et al. 2006).

Function.—The polar bear and *Tremarctos ornatus* have the lowest means for corpuscular volume (MCV) of red blood cells and the highest blood albumin level of all bears (Seal et al. 1970). Based on a sample of 62 bears of all species, *T. ornatus* possesses the smallest

MCV with an average of 55 fl ($n = 40$ —Seal et al. 1967; Castellanos et al. 2010). Blood cell size could be a response to seasonal changes and food availability for *T. ornatus* and the polar bear (Seal et al. 1967; Castellanos et al. 2010).

Male individuals ($n = 23$) had higher mean serum protein levels (155.6 g/L) than did females ($n = 23$, 132.8 g/L—Castellanos et al. 2010). Hematological values (mean \pm *SD*) for combined sexes of captive, reintroduced, and wild animals were: cholesterol 7.98 ± 1.97 mmol/L ($n = 33$), total protein 77.30 ± 15.30 g/L ($n = 27$), triglycerides 7.33 ± 1.64 mmol/L ($n = 34$), blood urea nitrogen 4.77 ± 1.51 mmol/L ($n = 29$), glutamic oxalic transaminase 30.23 ± 20.68 U/L ($n = 38$), glutamic pyruvic transaminase 21.43 ± 19.41 U/L ($n = 39$), alkaline phosphatase 97.57 ± 58.21 U/L ($n = 31$), calcium 1.87 ± 0.28 mmol/L ($n = 32$), phosphorus 1.68 ± 0.70 mmol/L ($n = 35$), glucose 3.56 ± 1.46 mmol/L ($n = 18$), urea 9.85 ± 4.48 mmol/L ($n = 38$), hematocrit 0.43 ± 0.05 L/L ($n = 45$), hemoglobin 144.45 ± 20.89 g/L ($n = 46$), leukocytes $9.11 \pm 2.98 \times 10^9$ /L ($n = 44$), erythrocytes $7.87 \pm 1.52 \times 10^{12}$ /L ($n = 37$), segmented leukocytes $6.47 \pm 0.94 \times 10^9$ /L ($n = 45$), lymphocytes $2.20 \pm 0.77 \times 10^9$ /L ($n = 44$), monocytes $0.13 \pm 0.13 \times 10^9$ /L ($n = 46$), eosinophiles $0.16 \pm 0.22 \times 10^9$ /L ($n = 43$), basophiles $0.01 \pm 0.05 \times 10^9$ /L ($n = 43$), band cells $0.027 \pm 0.11 \times 10^9$ /L ($n = 40$), mean cellular hemoglobin concentration 334.17 ± 43.10 g/L ($n = 36$), mean cellular hemoglobin 18.33 ± 3.03 pg ($n = 38$ —Nassar-Montoya et al. 1997; Castellanos et al. 2010).

ONTOGENY AND REPRODUCTION

Length at birth is 225–280 mm and weight is 300–500 g (Saporiti 1949; Roth 1964; Dathe 1967; Castellanos et al. 2016a). Neonates are black and toothless at birth, with closed

eyes. Eyes open completely by day 31 (Saporiti 1949). The only record of growth rate for young *Tremarctos ornatus* was presented by Saporiti (1949) as 50 mm/day.

Most of the information available for reproduction of *T. ornatus* has been obtained from captive individuals (Saporiti 1949; Roth 1964; Gensch 1965; Bloxam 1977; Michel et al. 1983; Kuhme 1991; Lengwinat et al. 2001; García-Rangel 2012). *T. ornatus* is a polyestrous species with facultative seasonal reproduction (Saporiti 1949; Mondolfi 1971; Spady et al. 2007; Enciso 2013) and is capable of embryonic diapause (Lengwinat et al. 2001; Knauf et al. 2003; Enciso 2013). After diapause, gestation length is short and difficult to calculate (Michel et al. 1983; Rosenthal 1987; Spady et al. 2007; García-Rangel 2012).

Captive females present 3–4 phases of ovarian activity per year (Enciso 2013). Wild females have an interval of 9 months between estrous cycles with a maximum of three cycles in 24 months (Spady et al. 2007). Duration of estrus is estimated at 5 days (Spady et al. 2007) but can vary depending on the latitude and associated photoperiod cycle of the facility (Knauf et al. 2003). Captive females from Brazil and Colombia had estrous cycles that lasted 3–10 days (Sanchez-Arbouin and Nassar-Montoya 1997; Enciso 2013).

Gestation varies from 120–254 days (Saporiti 1949; Gensch 1965; Bloxam 1977; Kuhme 1991; Castellanos 2015). Castellanos (2015) reported the shortest gestation period of 120–125 days, similar to the period reported for the sun bear (Frederick et al. 2012). Litter size varies from 1 to 3 young. Sexual maturity in females is attained at 4–7 years of age (Saporiti 1949; Dathe 1967; Bloxam 1977; Rosenthal 1987).

Tremarctos ornatus displays seasonal reproductive activity in wild individuals that corresponds to resource availability, but in captive individuals is associated with photoperiod

(Appleton et al. 2018). Births are concentrated in autumn in tropical latitudinal zones ($< 23.5^\circ$ N or S), whereas in mid-temperate latitudinal zones ($35\text{--}55^\circ$ N or S) most births occur during the winter (Peyton 1980; Rosenthal 1987; Spady et al. 2007; García-Rangel 2012; Appleton et al. 2018).

ECOLOGY

Population characteristics. —The few attempts at population estimates for *Tremarctos ornatus* have been derived from species such as the American black bear or from genetic analyses; some local approaches have been performed. The first approximation for population estimation was made by Peyton et al. (1998), resulting in a total wild population of 18,000–65,000 individuals across the entire range. Later, based on genetic analyses Ruiz-García (2003) estimated a global population size of 19,000–24,000 individuals. The majority of density estimations published before 2011 and mentioned in this account are discussed in detail by Garshelis (2011). Field-based density estimates for *T. ornatus* are preliminary and characterize sites from across its geographical range. In Venezuela, extrapolating from American black bear density data, Yarena and Torres (1994) estimated 0.04 individuals/km², values that Cáceres-Martínez et al. (2018) validated with field data in northern Colombia. Density was estimated at 0.03 individuals/km² in the eastern range (Cordillera Oriental) of the Andes in Colombia (Reyes et al. 2018; Rodríguez et al. 2019; Rodríguez et al. 2020). Viteri (2007) calculated densities between 0.03–0.07 individuals/km² and Molina et al. (2017) determined a similar value of 0.074 individuals/km², whereas an estimate of 0.039 individuals/km² was obtained by Morrell (2018) in northern Ecuador. Density calculations in Bolivia suggested slightly lower densities of 0.04–0.06 bears/km² (Ríos-Uzeda et al. 2007).

The greatest distance recorded for daily movements by an individual is 15 km in Bolivia (Rechberger et al. 2001). Daily movements between 800–2,435 m in elevation are common in Bolivia (Paisley 2001).

No records of longevity exist in wild individuals, but in captivity, *T. ornatus* can live as long as 40 years (Castellanos et al. 2016a). Sexual maturity in captivity is attained at 3–7 years (mean age for females = 4 years, mean age for males = 5 years—Rodríguez-Clark and Sánchez-Mercado 2006; García-Rangel 2012; Arias-Bernal and Yarto-Jaramillo 2019). Annual survival rates for neonates in captive populations are low (59–64%—Rodríguez-Clark and Sánchez-Mercado 2006). Fertility declines after 15 years of age and decreases rapidly after 25 years of age (Rosenthal 1987; Rodríguez-Clark and Sánchez-Mercado 2006).

Space use.—*Tremarctos ornatus* uses several habitat types, from scrub desert to subalpine páramos at elevations from 200 m to 4,170 m (Peyton 1980, 1981). *T. ornatus* shows a preference for higher elevation forest types such as montane humid forest, elfin, and Andean cloud forests (Mondolfi 1989; Cuesta et al. 2003; Ríos-Uzeda et al. 2006; Vela-Vargas et al. 2014; Filipczyková et al. 2016), high altitude grasslands (Goldstein 2002), páramos (Yerena and Torres 1994; Cuesta et al. 2003), pajonales, *Polylepis* forest (Azurduy and Velez-Liendo 2001) and oak forests (Otálora-Ardila 2003). Use of lower elevation habitats is rare, but Figueroa (2012) recorded seasonal use of tropical Amazon forest in Peru and tropical dry coastal forests (Appleton et al. 2018; Kleiner et al. 2018), with elevation ranges between 140–1,300 m.

Home ranges of two males in Bolivia were 6.6 km² and 7.4 km² (Paisley 2001). In Ecuador, home range estimates for a reintroduced male were larger than the average of two females (male = 61 km², female = 4.1 km²—Castellanos 2003; Castellanos et al. 2005). Home

range nearest-neighbor convex hull (K-NNCH) estimates for wild males ($n = 3$; $59 \pm 4.33 \text{ km}^2$) were on average 3 times larger than for females ($n = 5$; $15 \pm 5.35 \text{ km}^2$ —Castellanos 2011).

Diet.—Feeding strategies of *Tremarctos ornatus* vary based on four habitat characteristics: fruiting events, resource availability, geographical movements, and local migration (Figuroa 2013a; Gonzales et al. 2016; Cáceres-Martínez et al. 2020). Although its main diet is based on plant consumption, with 314 plant species identified (Chung 2006; García-Rangel 2012; Figuroa 2013a; 2013b), *T. ornatus* is considered to be an opportunistic omnivore (Figuroa 2013b; Gonzales et al. 2016), with high preference for consumption of plant meristematic tissues and fruits (Peyton 1980; Garcia and Betancur 2002; Goldstein 2004; Troya et al. 2004). Bromeliads (Bromeliaceae), palms (Araceae), bamboo (Poaceae), and fruits from Ericaceae and Lauraceae are the principal food items identified in the diet (García-Rangel 2012; Figuroa 2013a; Cáceres-Martínez et al. 2020). In dry areas of northern Perú, *T. ornatus* frequently consumes cacti, including: *Browningia microsperma*, *Melocactus peruvianus*, *Echinopsis pachanoi*, *Neoralmundia arequipensis gigantea*, *Opuntia ficus-indica*, *Echinocactus*, and *Mammillaria* (Figuroa and Stucchi 2008). *T. ornatus* is considered an agent to disperse seeds of species such as *Nectandra* cf. *cuneatocordata*, *Symplocos* cf. *cernuay*, and *Gaultheria vaccinioides* (Rivadeneira-Canedo 2008), and other species of Lauraceae (Peyton 1987) and *Styrax ovatus* (Styracaceae—Young 1990). *T. ornatus* consumes domestic crops such as corn (*Zea mays*), sugar cane (*Saccharum officinarum*), and plantain (*Musa paradisiaca*), generating conflicts with human communities (Peyton 1980; Peyton et al. 1998; Jorgenson and Sandoval-A 2005; Figuroa 2015a; Albarracín and Aliaga-Rossel 2018; Escobar-Lasso et al. 2020). In northern Colombia, *T. ornatus* showed a greater niche breadth during the dry season (July–

August and December–February) than in the wet season (March–June and September–November) and low overlap in the diet as evaluated using the Pianka Index ($O = 0.12$ —Cáceres-Martínez et al. 2020)

Different species of mammals were identified in scat samples from *T. ornatus*, with small rodents (*Akodon*, *Microryzomys*, and *Cavia* cf. *tschudii*) being most abundant (Gonzales et al. 2016). Other mammals registered in scats are medium-sized rodents, such as the Central American agouti (*Dasyprocta punctata*), nine-banded armadillo (*Dasybus novemcinctus*), coatis (*Nasua nasua* and *Nasuella olivacea*), and vicuñas (*Vicugna vicugna*—Cáceres-Martínez et al. 2020; Hernani-Lineros et al. 2020). Attacks on mountain tapirs (*Tapirus pinchaque*) have been reported in Colombia (Rodríguez et al. 2014) and scavenging on white-tailed deer (*Odocoileus virginianus*) reported in Peru (Van Horn et al. 2014). *T. ornatus* is considered to be a facultative carnivore that preys upon and scavenges both live animals and dead domestic animals, such as donkeys, cows, and sheep (Goldstein 2002; Goldstein et al. 2006; Figueroa 2013b; Parra-Romero et al. 2019). Fragments of plastic have also been recorded in scats at Tamá National Park, Colombia (Cáceres-Martínez et al. 2015).

Diseases and parasites.— In captive conditions, *Tremarctos ornatus* tends to develop alopecia syndrome, leading to partial or complete loss of hair due to unknown causes (Nassar-Montoya et al. 1997; Owen et al. 2009; Nicolau et al. 2018; Arias-Bernal and Yarto-Jaramillo 2019). The syndrome mostly seems to affect females in captive social housing conditions and has not been reported in wild individuals (Barbon 2013; Van Horn et al. 2019). Multiple types of neoplasia have been reported, including transitional cell carcinoma (Chandrasekar et al. 2016)

and thymoma (Cooper 1999), and other types of carcinomas (Nassar-Montoya et al. 1997; Arias-Bernal and Yarto-Jaramillo 2019).

Nematodes such as *Baylisascaris transfuga*, *Baylisascaris venezuelensis*, *Strongyloides*, *Ancylostoma*, and *Ascaris* have been detected in both captive (Schaul 2006; Luzuriaga 2014) and wild individuals (Figueroa 2015b; Guerrero and Castellanos 2016; Pérez Mata et al. 2016).

Castellanos et al. (2005) reported the potential death of one reintroduced *T. ornatus* in Ecuador due to tick fever caused by the hemoparasite *Babesia*. Distemper virus (*Morbillivirus*) resulted in the death in Europe of one captive *T. ornatus* cub (Schönbauer et al. 1984). Recorded protozoa parasites in wild and captive individuals include *Blastocystis*, *Cryptosporidium*, *Giardia*, *Coccidia*, and *Entamoeba* (Luzuriaga 2014; Figueroa 2015b). Only one record of ticks has been reported in *T. ornatus* (*Trichodectes ferrissi*—Cardozo-de-Almeida et al. 2003).

Interspecific interactions.—Interactions with both vertebrates and invertebrates have been reported. *Tremarctos ornatus* and mountain tapirs are frequently recorded in sympatric conditions in high-altitude ecosystems, such as Andean forest and páramo (Castellanos 2014), but one record of an attack by a *T. ornatus* on a mountain tapir exists (Rodríguez et al. 2014). When feral dogs (*Canis familiaris*) are present in areas where *T. ornatus* is present, occupancy rates of *T. ornatus* decrease and its diurnal activity patterns change too (Zapata-Ríos and Branch 2016, 2018). Dung beetles (*Uroxys brachialis*, *Uroxys depressifrons*, and *Uroxys nebulinus*: Scarabaeidae) fed on the dung of *T. ornatus* in the forest at La Planada Natural Reserve, southern Colombia (Escobar 2003).

HUSBANDRY

Tremarctos ornatus has been exhibited in captivity since 1903 when the first individual was displayed at Amsterdam Zoo (Cooper 1999). The captive population worldwide for 2017 was 255 individuals (129 males, 114 females, and 12 individuals with no reported sex) housed in 163 institutions (Anonymous 2017; Hall 2017).

Traditional chemical restraint protocols include ketamine (3–8 mg/kg body weight) and xylazine (2 mg/kg) and Yohimbine (Reversine S.A., Australia, New South Wales) as the reversal agent (0.1–0.25 mg/kg—Castellanos et al. 2016a). Protocols used at Bioparque Wakatá, Colombia, include ketamine (5.6–7.3 mg/kg), dexmedetomidine (0.02–0.035 mg/kg), and midazolam KDM (0.27–1.01 mg/kg) with the reversal agent atipamazole (0.2 mg/kg), flumazenil (0.01 mg/kg) via intravenous, $n = 5$; tiletamine-zolazepam (6–6.5 mg/kg), ketamine (2–6.2 mg/kg) with reversal agent flumazenil (0.01 mg/kg) via intravenous, $n = 6$; ketamine (4 mg/kg), medetomidine (0.04 mg/kg), and midazolam (0.1 mg/kg) with reversal agent atipamezole (0.24 mg/kg), flumazenil (0.01 mg/kg), $n = 2$ (Paisley 2001; Bourne et al. 2010; Arias-Bernal and Yarto-Jaramillo 2019).

Captive feeding protocols vary (Rosenthal 1987). At La Planada Natural Reserve (Colombia), captive individuals were fed with a corn soup base (milk, raw sugar honey, vegetables, calcium, eggs, meat, and liver emulsion). At Cologne Zoo (Germany), fruits and vegetables were offered, including carrots, apples, pears, and grapes. Based on wild diets, a solid diet called “chapo” was formulated for rehabilitation purposes (Castellanos et al. 2016a). For a 60 kg bear, daily quantities were: 3 kg of mixed fruits (banana, papaya, and seasonal staples), guava (500 g), oat (340 g), wheatgerm (260 g), and mineralized salt (30 g). As the animal

rehabilitates, the formula is adjusted over time with increasing amounts of wild food items (Castellanos et al. 2016a)

In a feeding trial, two captive animals consumed 1.6% of their body weight in dry matter daily, with an average digestibility of 60.5%. Apparent digestion coefficients for neutral detergent fiber, crude protein, soluble sugars, and crude fat were 12.8%, 70%, 80.3%, and 64%, respectively. Gastrointestinal transit was measured at 8–24 hours, leading researchers to hypothesize that wild *T. ornatus* consumed high-fiber foods, whereas captive bears tended to select low-fiber ingredients in their diets (Goldman et al. 2001).

Cage requirements for captive *T. ornatus* are listed in Bloxam (1977), with an outdoor space of 267 m², a swimming pool 32.5 m² in diameter and a depth of 1.5 m. Sleeping dens should be on average 3.2 m in length by 2.65 m in width by 2.4 m in height (Bloxam 1977; Peel et al. 1979). Requirements for rehabilitation enclosures were reviewed extensively in Castellanos et al. (2016a).

BEHAVIOR

Grouping behavior.—*Tremarctos ornatus* is generally solitary, but forms temporary pairs during mating periods (Mondolfi 1971; Peyton 1999; Castellanos et al. 2005; García-Rangel 2012; Appleton et al. 2018). When food resources are concentrated, *T. ornatus* sometimes forms rudimentary social groups to exploit crops or crop waste (Figuroa 2015a), or to scavenge livestock (Paisley 2001; Parra-Romero et al. 2019).

Reproductive behavior.— Descriptions of mating behaviors are scarce and focus mostly on captive individuals. Normal behavior includes nonaggressive fights and multiple copulations (2–8 copulations) over intervals of 8–60 min (Bloxam 1977).

During pregnancy, females construct and use dens. The den is about 2 m long and 1 m wide with a sheltered depression in the middle that is 1.5 m long, 800 mm wide, and 500 mm deep (Castellanos 2010). The area surrounding the den is clean with no feces or strong odors present in order to avoid attracting potential predators. The den is used for about 9–12 weeks after the birth (Mondolfi 1971; Castellanos et al. 2016a). Dens may be used throughout the year as the young mature (Castellanos 2010). While nursing, females may leave maternal dens for up to 48 hours to seek food. The length of time away from the young may be due to anthropogenic effects of habitat loss, with greater times away in areas with greater habitat loss. Adult females may even abandon young for extended periods of time due to lack of resources (Castellanos et al. 2019).

Communication.—Males apply chemical scent-marks to a variety of tree species for self-advertisement and potentially to mark territories (although this is an untested hypothesis), whereas females do not scent-mark perhaps due to risk of cannibalism by males (Filipczyková et al. 2016). In dry areas of Peru, *Tremarctos ornatus* concentrates tree rubbing areas close to waterholes (Kleiner et al. 2018).

Sound spectrograms show that vocalizations are composed of tonal and atonal elements with ranges from 0.01–7 kHz. Two reintroduced *T. ornatus*, produced six types of sounds that were characterized as follows: guttural sounds when individuals were curious (kurrrrr, tuutucttt), screams when the animals fought for food, small chuffs when animals attacked other individuals, and whining sounds (eggmmmmm) when the animals were found in the forest canopy. A male produced a particular sound when masturbating (MMrnnMMrnn). This unique sound could be heard at least 30 m away (Castellanos 2003; Castellanos et al. 2005). Captive cubs produced a

particular vocalization called humming, which had a main frequency < 2 kHz and was produced on average over 3.6 seconds, associated with comfort or contentment (Peters et al. 2007).

Communication between mother and young was recorded by Elowson (1988) in captive conditions. Trill calls from the mother ($n = 23$) were recorded with a peak frequency of (n ; mean $\pm SD$) 418 ± 39 Hz and growls ($n = 2$; 175 ± 35 Hz). Cub sounds were characterized into five types including trills ($n = 33$; 375 ± 104 Hz), yelp ($n = 15$; 817 ± 331 Hz), whimper ($n = 39$; 347 ± 181 Hz), squeals (long and short) with frequency peaks of $2,000 \pm 1,471$ and $1,493 \pm 718$ Hz, and screams (long and broad ($n = 15$), short and broad ($n = 20$), long narrow ($n = 9$)) with frequencies of $1,312 \pm 648$ Hz, $1,279 \pm 726$ Hz, and 328 ± 86 Hz, respectively.

Miscellaneous behavior.— *Tremarctos ornatus* is mostly diurnal with activity peaks between 600 to 1000 h (Paisley and Garshelis 2006; Parra-Romero et al. 2019). In Ecuador, activity patterns changed from a bimodal distribution of activity in absence of feral dogs to more diurnal activity concentrated between 1200 h to 1400 h if feral dog packs were present (Zapata-Ríos and Branch 2016).

Cannibalism is rare, but two cases have been reported in Ecuador. In one instance, a wild *T. ornatus* was shot by a hunter and later consumed by other bears (Castellanos 2006). Another incident occurred at Cayambe Coca National Park (Ecuador), where a reintroduced *T. ornatus* female was found dead with signs of predation attributed to a large male bear (Castellanos et al. 2016b).

Tree nests consist of a platform and an oval depression at the top of the nest; different tree species, such as *Benchesia*, *Ficus*, *Cedrela*, *Clusia*, and *Podocarpus* are used. Nest locations

have been associated with consumption of fruit, resting, and areas close to livestock (Peyton 1980; Goldstein 1991, 2002; Peyton et al. 1998).

GENETICS

Cytogenetics.—Although all the Ursine bears have 74 chromosomes and Ailuropodinae has 42, the karyotype of *Tremarctos ornatus* is completely different (Nash and O'Brien 1987; Garshelis 2009). *T. ornatus* has a diploid number (2n) of 52 largely bi-armed chromosomes, with 16 pairs of metacentric autosomes and 9 pairs of acrocentric autosomes (Newnham and Davidson 1966, 1967; Nash and O'Brien 1987). The X chromosome is relatively large and metacentric, and the Y chromosome is smaller and acrocentric (Newnham and Davidson 1967).

Tremarctos ornatus diverged from an ancestor with the ursine karyotype (2n = 74) about 10.91 million years ago (9.93-11.89 million years ago) and differs from that of the presumed ancestor by two fusions, two fissions, 11 centric fusion,s and one inversion (Nash and O'Brien 1987; Tian et al. 2004; Wienberg 2004; Yu et al. 2007; Garshelis 2009).

Molecular genetics.— Mitochondrial genome length was 16,766 base pairs in *Tremarctos ornatus* (Yu et al. 2007). Fecal sampling using the PCR amelogenin gene with primers SE47-SE48 had a 100% success rate in determining the sex of the individuals (Caselli and Maturrano 2016).

Genetic diversity parameters of microsatellite data showed that *T. ornatus* had a moderate mean number of alleles per microsatellite locus and moderate expected heterozygosity (H_e 0.382 \pm 0.298—Ruiz-Garcia 2003; Ruiz-Garcia et al. 2003; Ruiz Garcia et al. 2005; Viteri 2007; Zhang et al. 2007). Haplotype diversity calculations for the Ecuador population were 0.5–0.705 (Viteri and Waits 2009; Cueva et al. 2018) and overall for South America were calculated as

0.980 ± 0.016 (Arias-Vásquez 2017). Recent studies revealed that *T ornatus* is divided into two evolutionary significant units (ESUs) with an overall haplotype diversity of 0.914 ± 0.013 and nucleotide diversity (π) of 0.0191 ± 0.0126, average microsatellite H was 0.55, lower than in other bear species (Ruiz-García et al. 2020a).

For the 551 individuals in captivity, expected heterozygosity was calculated as $H_e = 0.97$, with an inbreeding coefficient of 0.20 (Rodríguez-Clark and Sánchez-Mercado 2006). These values are the result of a pedigree analysis, considering only live, reproductive individuals and their direct ancestors, these results are based on software analyses and not derived from any genetic sampling approximation.

Population genetics.—Population genetics for *Tremarctos ornatus* is poorly known. Populations do not appear to be in Hardy-Weinberg equilibrium and a high level of homozygosity and genetic isolation exists among populations (Ruiz-Garcia 2003; Ruiz Garcia et al. 2005).

Genetic structure of *T. ornatus* in Ecuador showed high haplotypic diversity ($H_d = 0.845 \pm 0.033$) whereas microsatellite diversity was moderate ($H = 0.584 \pm 0.188$), demonstrating that genetic structure of the species in Ecuador is homogeneous and has not been affected by the presence of the Andes range, suggesting that *T. ornatus* in Ecuador should be considered as an unique management unit (Ruiz-García et al. 2020c). The same study was performed in Colombia (Ruiz-García et al. 2020b) and showed a similar haplotypic diversity in a sample of 108 wild individuals ($H_d = 0.895 \pm 0.018$) with higher microsatellite diversity than in Ecuador ($H = 0.645 \pm 0.211$).

Arias-Vasquez (2017) identified three well-differentiated phylogeographic groups: 1) southern Colombia, 2) northern Andes (Venezuela, Colombia, Ecuador, and northern Peru), and 3) southern Andes (southern Peru and Bolivia). Based on a sample of 294 wild individuals, two evolutionary significant units were identified: a Northern Andean Clade (Venezuela, Colombia, Ecuador, and middle-northern Peru) and the Southern Andean Clade (southern Peru and northern and middle area of the Bolivian Andes—Ruiz-García et al. 2020a). Ruiz-García et al. (2003) estimated the effective population size as $N_e = 19,681$ individuals across the range of the species.

CONSERVATION

Tremarctos ornatus is assessed as “Vulnerable” (VU) by the International Union for Conservation of Nature and Natural Resources Red List of Threatened Species (Velez–Liendo and García-Rangel 2017), maintaining the same category since 1982. Furthermore, *T. ornatus* has been included in CITES Appendix I since 1975. The population trend is estimated to be decreasing, with about 2,500-10,000 individuals across its geographic distribution (Velez-Liendo and García-Rangel 2017). All countries have implemented hunting bans; however, enforcement often is poor (García-Rangel 2012; Figueroa 2014). Nevertheless, conservation action plans have been proposed for Venezuela, Colombia, and Ecuador, a national assessment has been prepared for Bolivia, and education and conservation programs have been conducted in Bolivia, Peru, Colombia, and Venezuela (Ministerio Del Medio Ambiente 2001; Rodriguez et al. 2003; Yerena 2014; SERFOR 2016; Velez–Liendo and García-Rangel 2017; Parques Nacionales Naturales de Colombia and Wildlife Conservation Society 2018; Ministerio del Ambiente y Agua del Ecuador

2020). Most programs, however, encounter implementation challenges due to a shortage of funding.

The most significant threats for *T. ornatus* across its range include habitat loss and fragmentation, illegal killing, and conflicts with humans, whether real or perceived (Kattan et al. 2004; Sánchez-Mercado et al. 2008; Jampel 2016; Zukowski and Ormsby 2016; Velez–Liendo and García-Rangel 2017; Bazantes-Chamorro et al. 2018; Parra-Romero et al. 2019). Nonetheless, climate change also is a critical threat for *T. ornatus*, especially through the impact on the upper elevation ecosystems that it uses (Velez–Liendo and García-Rangel 2017). Current estimates of habitat loss have identified Venezuela as the country with the greatest projected loss, followed by Peru, Colombia, and Ecuador (Kattan et al. 2004; Sánchez-Mercado et al. 2014; Velez–Liendo and García-Rangel 2017; Bazantes-Chamorro et al. 2018; Guerrero-Casado and Zambrano 2020). Habitat loss is mainly due to inappropriate agricultural practices, expansion of the agricultural and cattle frontier, ineffective land and agrarian reforms and violence control, expansion of illegal crops, and mining and oil exploitation. Roads and other human infrastructure also fragment the habitat (Armenteras et al. 2003, 2011; Dávalos et al. 2011; García-Rangel 2012; Velez–Liendo et al. 2014; Chadid et al. 2015; Velez–Liendo and García-Rangel 2017; Zapata-Ríos and Branch 2018). Illegal killing by livestock owners is mostly due to retaliation following depredation, but *T. ornatus* also is harvested for illegal commercial trade and for use in traditional medicine. In Perú illegal trade of bear fat and body parts was recorded in 27 rural markets in 14 regions of the country with a range of prices between U.S.\$ 0.90 (20 ml of fat), U.S.\$ 14.5 (180 ml of blood) and U.S.\$ 43 (skin—Figuroa 2014). No estimates exist for the number of individuals killed, but substantial numbers may be taken

(Figueroa 2014; Sánchez-Mercado et al. 2014; Velez–Liendo and García-Rangel 2017; Andrade et al. 2019).

Overall, conservation of *T. ornatus* represents a significant challenge for all the countries across its geographic distribution. Not only are the threats continuing to increase along its geographic range, the intrinsic vulnerability of the specific habitats in which *T. ornatus* thrives represents a major challenge to preserve (Crespo-Gascón and Guerrero-Casado 2019; Guerrero-Casado and Zambrano 2020).

ACKNOWLEDGMENTS

Thanks to the following: Dr. Noe de la Sancha for his assistance with the pictures of the skull from the Field Museum of Natural History and Angela Hurtado for her assistance on the photo editing process; Luis Guillermo Linares for allowing use of the photograph of a wild specimen from Chingaza National Protected Area in Colombia; Dr. Peter Lurz for his help in the translation of several German documents; Dr. Jairo Pérez-Torres for facilitating information about the species; and Dr. Pamela R. Owen by her comments and clarifications on the fossil record. JPJ wishes to acknowledge the following individuals for their support over the years: Jorge Ignacio “El Mono” Hernández-Camacho (deceased), Federico Medem-Medem (deceased), Bernard Peyton, Ernesto Barriga-Bonilla, José Vicente Rodríguez-Mahecha, and Amanda Barrera de Jorgenson. IMVV acknowledges the financial support provided by the COLCIENCIAS-Fulbright program in Colombia and the College of Agriculture and Life Sciences of the University of Arizona. *The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

The authors acknowledge the comments from two anonymous reviewers and Dr. Meredith Hamilton.

LITERATURE CITED

- AGNARSSON, I., M. KUNTNER, AND L. J. MAY-COLLADO. 2010. Dogs, cats, and kin: A molecular species-level phylogeny of Carnivora. *Molecular Phylogenetics and Evolution* 54:726–745.
- ALBARRACÍN, V., AND E. ALIAGA-ROSSEL. 2018. Bearly guilty: Understanding human–Andean bear conflict regarding crop losses. *Ethnobiology Letters* 9:323–332.
- ALBARRACÍN, V., S. PAISLEY, E. ALIAGA-ROSSEL, AND X. VÉLEZ-LIENDO. 2013. State of Andean bear (*Tremarctos ornatus*) in Bolivia. P. 739 in *Molecular population genetics, evolutionary biology, and biological conservation of Neotropical Carnivores* (M. Ruiz-Garcia and J. Shosteli, eds.). Nova Publishers, New York.
- ALBERICO, M., A. CADENA, J. HERNÁNDEZ-CAMACHO, AND Y. MUÑOZ-SABA. 2000. Mamíferos (Synapsida: Theria) de Colombia. *Biota Colombiana* 1:43–75.
- ALLEN, G. 1942. Extinct and vanishing mammals of the western hemisphere with the marine species of all the oceans. American Committee for International Wildlife Protection. Special Publication 11-1: 1-620.
- ANDERSON, S. 1997. Mammals of Bolivia, taxonomy and distribution. *Bulletin of the American Museum of Natural History* 231:1–652.
- ANDRADE, M., G. ESPINOZA, AND J. MONCADA. 2019. Percepción de actores clave acerca del conflicto ser humano-oso en la parroquia Plaza Guitierrez, Íntag, Imbabura, Ecuador. *Mammalia aequatorialis* 1:43–50.
- Anonymous. 2017. International studbooks for rare species of wild animals in captivity.

- International Zoo Yearbook 51:458–488.
- APPLETON, R. D., R. C. VAN HORN, K. V. NOYCE, T. J. SPADY, R. R. SWAISGOOD, AND P. ARCESE. 2018. Phenotypic plasticity in the timing of reproduction in Andean bears. *Journal of Zoology* 305:196–202.
- ARIAS-BERNAL, L., AND E. YARTO-JARAMILLO. 2019. Medicine of captive Andean bears. Pp. 548–554 in Miller - Fowler's zoo and wild animal medicine current therapy (E. Miller, N. Lamberski, and P. Calle, eds.). Vol 9. Saunders, Philadelphia, Pennsylvania.
- ARIAS-VÁSQUEZ, J. Y. 2017. Análisis filogeográfico del Oso Andino (*Tremarctos ornatus*) a través de todo su rango geográfico de distribución mediante tres genes mitocondriales. M.S thesis. Pontificia Universidad Javeriana, Bogotá. Colombia.
- ARMENTERAS, D., F. GAST, AND H. VILLAREAL. 2003. Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological Conservation* 113:245–256.
- ARMENTERAS, D., N. RODRÍGUEZ, J. RETANA, AND M. MORALES. 2011. Understanding deforestation in montane and lowland forests of the Colombian Andes. *Regional Environmental Change* 11:693–705.
- AZURDUY, C., AND X. VELEZ-LIENDO. 2001. Nota sobre presencia, uso e importancia de los bosques de *Polylepis* como parte del habitat del oso andino (*Tremarctos ornatus*) en la cuenca alta del Río Cañón. *Revista Boliviana de Ecología* 9:79–84.
- BARBON, A. 2013. Alopecia syndrome in a spectacled bear (*Tremarctos ornatus*): a case report. *Solitaire* 24:14–18.
- BAZANTES-CHAMORRO, J., N. REVELO-MORÁN, AND J. MONCADA-RANGEL. 2018. Conflicto

- humano–oso andino (*Tremarctos ornatus*) en San Francisco de Sigüipamba, Provincia de Imbabura, Ecuador. *Revista Mexicana de Mastozoología* 8:81–95.
- BININDA-EMONDS, O. R. P. 1998. Towards comprehensive phylogenies: examples within the Carnivora (Mammalia). Ph.D. dissertation, University of Oxford. Oxford, United Kingdom.
- BISBAL, F. J. 1993. Human impact on the carnivores of Venezuela. *Studies on Neotropical Fauna and Environment* 28:145–156.
- BLOXAM, Q. 1977. Breeding the spectacled bear *Tremarctos ornatus* at Jersey zoo. *International Zoo Yearbook* 17:158–161.
- BOURNE, D. C., J. M. CRACKNELL, AND H. J. BACON. 2010. Veterinary issues related to bears (Ursidae). *International Zoo Yearbook* 44:16–32.
- CABRERA, A. 1957. Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’* 4:iv + 308.
- CABRERA, A., AND J. YEPES. 1940. Mamíferos sudamericanos. Vida, costumbres y descripción. Compañía Argentina de Editores, Buenos Aires. Argentina.
- CÁCERES-MARTÍNES, C., A. ACEVEDO-RINCÓN, J. F. GONZÁLEZ-MAYA, AND L. R. SÁNCHEZ-MONTANO. 2018. State of knowledge and strategies of conservation of the Andean Bear (*Tremarctos ornatus*) in the northeast of Colombia. P. 26 in *Proceedings of the 25th Conference on Bear Research and Management* (S. Molina et al., eds.). Quito, Ecuador.
- CÁCERES-MARTÍNEZ, C. H., A. A. ACEVEDO, J. F. GONZÁLEZ-MAYA, C. H. CACERES-MARTÍNEZ, A. A. ACEVEDO RINCÓN, AND J. F. GONZÁLEZ-MAYA. 2016. Terrestrial medium and large-sized mammal’s diversity and activity patterns from Tamá National Natural Park and buffer zone, Colombia. *Therya* 7:285–298.

- CÁCERES-MARTÍNEZ, C. H., A. A. ACEVEDO-RINCÓN, AND L. R. SÁNCHEZ-MONTAÑO. 2015. Registros de plásticos en la ingesta de *Tremarctos ornatus* (Carnívora: Ursidae) y de *Nasuella olivacea* (Carnívora: Procyonidae) en el Parque Nacional Natural Tamá, Colombia. *Revista Mexicana de Biodiversidad* 86:839–842.
- CÁCERES-MARTÍNEZ, C. H., L. R. SÁNCHEZ MONTANO, A. A. ACEVEDO, AND J. F. GONZÁLEZ-MAYA. 2020. Diet of Andean bears in Tamá National Natural Park, Colombia. *Ursus* 31:1–11.
- CARDOZO-DE-ALMEIDA, M., P. M. LINARDI, AND J. COSTA. 2003. The type specimens of chewing Lice (Insecta, Mallophaga) deposited in the entomological collection of Instituto Oswaldo Cruz, Rio de Janeiro, RJ, Brazil. *Memorias do Instituto Oswaldo Cruz* 98:233–240.
- CARO, T. 2009. Contrasting coloration in terrestrial mammals. *Philosophical Transactions of the Royal Society* 364:537–548.
- CASELLI, C., AND L. MATURRANO. 2016. Sexaje molecular a partir de heces en osos de anteojos (*Tremarctos ornatus*). *Revista de Investigaciones Veterinarias del Peru* 27:252–258.
- CASTELLANOS, A. 2003. Ecology of re-introduced Andean bears in the Paquipucuna Biological Reserve, Ecuador: conservation implications. *Re-introduction News* 23:32–34.
- CASTELLANOS, A. 2006. Cannibalism in Andean bears? *International Bear News* 15:20–21.
- CASTELLANOS, A. 2010. Andean bear den found in Cloud forest. *International Bear News* 19:4–6.
- CASTELLANOS, A. 2011. Andean bear home ranges in the Intag region, Ecuador. *Ursus* 22:65–73.
- CASTELLANOS, A. 2014. Co-occurrence of Andean bear and mountain tapir at Papallacta region, Cayambe-Coca National Park, Ecuador: A brief description. *International Bear News*

23:20–21.

CASTELLANOS, A. 2015. Maternal behavior of a female Andean bear in the Paramo of cayambe Coca National Park, Ecuador. *International Bear News* 24:32–33.

CASTELLANOS, A., L. ARIAS, D. JACKSON, AND R. CASTELLANOS. 2010. Hematological and serum biochemical values of Andean bears in Ecuador. *Ursus* 21:115–120.

CASTELLANOS, A., D. A. JACKSON, AND L. ARIAS L. 2016a. Guidelines for the rescue, rehabilitation , release and post-release monitoring of Andean bears. Andean Bear Foundation. Quito, Ecuador.

CASTELLANOS, A., M. PILLAJO, AND F. TORRES. 2016b. Andean Bear Cannibalism in northern Ecuador. *International Bear News* 25:28.

CASTELLANOS, A. P., M. B. ALTAMIRANO, AND G. A. TAPIA. 2005. Ecología y comportamiento de osos andinos reintroducidos en la reserva biológica Maquipucuna, Ecuador: Implicaciones en la conservación. *Politécnica* 26.

CASTELLANOS, A. X., D. A. JACKSON, AND M. ASCANTA. 2019. Are reports of cub abandonment in Andean bears a result of increasing human encroachment? *International Bear News* 28:14–15.

CHADID, M. A., L. M. DÁVALOS, J. MOLINA, AND D. ARMENTERAS. 2015. A Bayesian spatial model highlights distinct dynamics in deforestation from coca and pastures in an Andean biodiversity hotspot. *Forests* 6:3828–3846.

CHANDRASEKAR, M., A. A. BHAT, AND C. BALACHANDRAN. 2016. Transitional cell carcinoma of the urinary bladder in a spectacled bear (*Tremarctos ornatus*). *Indian Veterinary Journal* 93:52–54.

- CHRISTIANSEN, P. 2007. Canine morphology in the larger Felidae: Implications for feeding ecology. *Biological Journal of the Linnean Society* 91:573–592.
- CHRISTIANSEN, P. 2008a. Evolution of skull and mandible shape in cats (Carnivora: Felidae). *PLoS ONE* 3:e2807.
- CHRISTIANSEN, P. 2008b. Feeding ecology and morphology of the upper canines in bears (Carnivora: Ursidae). *Journal of Morphology* 269:896–908.
- CHRISTIANSEN, P., AND S. WROE. 2007. Bite forces and evolutionary adaptations to feeding ecology in carnivores. *Ecology* 88:347–358.
- CHUNG, C. L. 2006. Contribución al conocimiento de los hábitos alimentarios del oso andino, *Tremarctos ornatus*, en el bosque montano Bosques de Ramos, Ayabaca-Piura. Departamento de Mastozoología, Museo de Historia Natural “Javier Prado”. UNMSM:12.
- COOPER, J. 1999. A thymona in an Andean bear *Tremarctos ornatus*. *Dodo* 35:67–69.
- COSSE, M., J. F. DEL MORAL SACHETTI, N. MANNISE, AND M. ACOSTA. 2014. Genetic evidence confirms presence of Andean bears in Argentina. *Ursus* 25:163–171.
- CRESPO-GASCÓN, S., AND J. GUERRERO-CASADO. 2019. The role of the spectacled bear (*Tremarctos ornatus*) as an umbrella species for Andean ecoregions. *Wildlife Research* 46:176–183.
- CUESTA, F., M. F. PERALVO, AND F. T. VAN MANEN. 2003. Andean bear habitat use in the Oyacachi River Basin, Ecuador. *Ursus* 14:198–209.
- CUEVA, D. F., B. GUTIERREZ, G. BRUQUE, S. MOLINA, AND M. L. TORRES. 2018. Mitochondrial DNA reveals low genetic diversity in Ecuadorian Andean bears. *Ursus* 29:43–50.
- CUVIER, F. 1825. Ours des Cordilleres du Chill. *Histoire Naturelle des Mammifères, avec des*

- figures originales, coloriées, dessinées d'après des animaux vivans. (G. Saint-hilaire & F. Cuvier, eds.). 50th edition. Published under the authority of the administration of Muséum d'Histoire Naturelle, France, Paris.
- DATHE, V. H. 1967. Bemerkungen zur Aufzucht von Brillenbären, *Tremarctos ornatus* (Cuv.), in Tierpark Berlin. Zoologische 34:105–133.
- DÁVALOS, L. M., A. C. BEJARANO, M. A. HALL, H. L. CORREA, A. CORTHALS, AND O. J. ESPEJO. 2011. Forests and drugs: Coca-driven deforestation in tropical biodiversity hotspots. Environmental Science and Technology 45:1219–1277.
- DAVIS, D. 1955. Masticatory apparatus in the spectacled bear *Tremarctos ornatus*. Fieldiana Zoology 37:25–46.
- DAVIS, D. 1958. Tarsal ligaments of the spectacled bear *Tremarctos ornatus*. Fieldiana: Zoology 39:91–105.
- ELOWSON, M. 1988. Mother/Cub vocal communication in the captive Spectacled bear (*Tremarctos ornatus*). P. 132 in Proceedings of the First International Symposium on the Spectacled bear. Chicago, USA.
- EMSLIE, S. 1995. The fossil record of *Arctodus pristinus* (Ursidae: Tremarctinae) in Florida. Bulletin of the Florida State Museum. Biological Sciences. 37:501–514.
- ENCISO, M., AND M. VÁSQUEZ. 2007. Some observations on Andean bears (*Tremarctos ornatus*) ovaries. International Bear News 16:13–14.
- ENCISO, M. H. 2013. Caracterização da atividade ovariana no Urso-de-óculos (*Tremarctos ornatus* Cuvier, 1825) mediante análise de metabólitos fecais de esteróides sexuais. M.S. thesis. Universidade de São Paulo. São Paulo. Brazil

- ENCISO, M. H., L. L. BERMÚDEZ, S. V. EVANGELISTA, G. M. ROJAS, AND W. L. HUANCA. 2006. Estudio preliminar de colección de semen en oso de anteojos (*Tremarctos ornatus*). Revista de investigaciones veterinarias del Perú 17:77–80.
- ESCOBAR, F. S. 2003. Feeding habits and distributional records of 11 Species of neotropical Scarabaeinae (Coleoptera: Scarabaeidae). The Coleopterists Bulletin 57:131–132.
- ESCOBAR-LASSO, S., J. CEPEDA-DUQUE, M. GIL-FERNANDEZ, AND J. F. GONZÁLEZ-MAYA. 2020. Is the banana ripe? - Andean bear-human conflict in a protected area of Colombia. Human - Wildlife Interactions 14:1–17.
- FALCONI, N. 2019. Spectacled bear database for Peru. Version 1.4. Department of Environmental Conservation, University of Massachusetts, Amherst.
<https://www.gbif.org/es/dataset/375eb3fe-af43-4d37-815a-d8bd891e8ca5>
- FALCONI, N., T. K. FULLER, S. DESTEFANO, AND J. F. ORGAN. 2020. An open access, occurrence database for Andean bears in Peru. Ursus 31:1–7.
- FIGUEIRIDO, B., P. PALMQVIST, AND J. A. PÉREZ-CLAROS. 2009. Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: An approach based on geometric morphometrics. Journal of Zoology 277:70–80.
- FIGUEROA, J. 2012. Presencia del oso andino *Tremarctos ornatus* (Carnivora: Ursidae) en el bosque Tropical amazónico del Perú. Acta Zoológica Mexicana 28:594–606.
- FIGUEROA, J. 2013a. Composición de la dieta de Oso Andino *Tremarctos ornatus* (Carnivora: Ursidae) en nueve áreas naturales protegidas del Perú. Therya 4:327–359.
- FIGUEROA, J. 2013b. Revisión de la dieta del Oso Andino *Tremarctos ornatus* (Carnivora: Ursidae) en America del Sur nuevos registros para Perú. Revista Museo Argentino de

- Ciencias Naturales 15:1–27.
- FIGUEROA, J. 2014. Tráfico de partes e individuos del oso andino *Tremarctos ornatus* en el Perú. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 38:177–190.
- FIGUEROA, J. 2015a. Interacciones humano–oso andino *Tremarctos ornatus* en el Perú: consumo de cultivos y depredación de ganado. *Therya* 6:251–278.
- FIGUEROA, J. 2015b. New records of parasites in free-ranging Andean bears from Peru. *Ursus* 26:21–27.
- FIGUEROA, J., AND M. STUCCHI. 2008. Las cactáceas en la dieta del oso andino *Tremarctos ornatus* en el Perú. *Quepo* 22:21–28.
- FIGUEROA, J., AND M. STUCCHI. 2013. Presencia del oso andino *Tremarctos ornatus* (Carnivora:Ursidae) en el corredor de conservación Vilcabamba-Amboró, sureste del Perú. *Therya* 4:511–538.
- FILIPCZYKOVÁ, E., I. HEITKÖNIG, A. CASTELLANOS, W. HANTSON, AND S. STEYAERT. 2016. Marking behavior of Andean bears in an Ecuadorian cloud forest: a pilot study. *Ursus* 27:122–128.
- FITZGERALD, C., AND P. R. KRAUSMAN. 2002. *Helarctos malayanus*. *Mammalian Species* 696:1–5.
- FLOREZ, Y. 1975. Excavaciones en el Mirador, Pacopampa. Seminario de Historia Rural Andino. Lima, Perú.
- FORSTENPOINTNER, G., AND G. E. WEISSENGRUBER. 2000. Morphological considerations on pharyngeal pouches in bears (Ursidae). *Advances in Ethology* 35:62.
- FREDERICK, C., K. E. HUNT, R. KYES, D. COLLINS, AND S. K. WASSER. 2012. Reproductive timing

- and aseasonality in the sun bear (*Helarctos malayanus*). *Journal of Mammalogy* 93:522–531.
- GARCÍA-RANGEL, S. 2012. Andean bear *Tremarctos ornatus* natural history and conservation. *Mammal Review* 42:85–119.
- GARCIA, N., AND J. BETANCUR. 2002. Dos especies nuevas de *Tillandsia* (Bromeliaceae). *Caldasia* 24:1–7.
- GARSHELIS, D. L. 2009. Family Ursidae. Pp. 448–497 in *Handbook of the mammals of the world: Carnivores* (E. Wilson and R. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.
- GARSHELIS, D. L. 2011. Andean bear density and abundance estimates — How reliable and useful are they? *Ursus* 22:47–64.
- GENSCH, W. 1965. Birth and rearing of a spectacled bear (*Tremarctos ornatus*) at Dresden Zoo. *International Zoo Yearbook* 5:111.
- GERVAIS, P. M. 1855. *Histoire naturelle de mammifères avec l'indication de leurs moeurs, et de leurs rapports avec les arts, le commerce et l'agriculture*. L. Curmer, Paris. France
- GILL, T. 1874. On the genera *Tremarctos*, Gervais (*Nearctos*, Gray), and *Aelurina*, Gervais (*Ailurogale*, Fitz). *The Annals and Magazine of Natural History, including Zoology, Botany and Geology* 13:15–16.
- GOLDMAN, I., S. SILVER, AND E. DIERENFELD. 2001. Passage and digestion in the spectacled bear (*Tremarctos ornatus*) fed a Zoo-based diet moderately high in fiber. P. 250 in *Proceedings of the American Zoo and Aquarium Association (AZA) Nutrition Advisory Group Fourth Conference on Zoo and Wildlife Nutrition* (M. Edwards, K. Lisi, M. Schegel and R. Bray, eds.). Fourth NAG Conference Publications, Lake Buena Vista, Florida.

- GOLDSTEIN, I. 1991. Are spectacled bear's tree nest feeding platform or resting places?
Mammalia 55:433–434.
- GOLDSTEIN, I. 1992. Distribución., presencia y conservación del Oso Frontino en Venezuela.
Biollania 9:171–182.
- GOLDSTEIN, I., V. GUERRERO, AND R. MORENO. 2008. Are there Andean bears in Panamá? Ursus
19:185–189.
- GOLDSTEIN, I., S. PAISLEY, R. WALLACE, J. P. JORGENSEN, F. CUESTA, AND A. CASTELLANOS.
2006. Andean bear-livestock conflicts: A review. Ursus 17:8–15.
- GOLDSTEIN, I. R. 2002. Andean bear-cattle interactions and tree nest use in Bolivia and
Venezuela. Ursus 13:369–372.
- GOLDSTEIN, I. R. 2004. Andean bear use of the epiphytic bromeliad *Tillandsia fendleri* at
Quebrada el Molino, Venezuela. Ursus 15:54–56.
- GONZALES, F. N., J. NEIRA-LLERENA, G. LLERENA, AND H. ZEBALLOS. 2016. Small vertebrates in
the spectacled bear's diet (*Tremarctos ornatus* Cuvier, 1825) in the north of Peru. Revista
Peruana de Biología 23:61–66.
- GOTCH, A. 1979. Mammals, their Latin names explained : a guide to animal classification.
Blandford Press, Poole, United Kingdom.
- GRAY, J. E. 1864. A revision of the genera and species of ursine animals (Ursidae), founded on
the collection of the British Museum. Proceedings of the Zoological Society of
London:677–709.
- GRAY, J. E. 1873. On the skull of the spectacled bear of Peru and of the *Helarctos* from Malacca
and Java. The Annals and Magazine of Natural History, including Zoology, Botany and

Geology 12:182–183.

- GUERRERO, R., AND A. CASTELLANOS. 2016. First Record of *Baylisascaris transfuga* (Nematoda : Ascarididae) in an Andean Bear (*Tremarctos ornatus*) Ecuador. International Bear News 25:24.
- GUERRERO-CASADO, J., AND R. H. ZAMBRANO. 2020. The worrisome conservation status of ecosystems within the distribution range of the spectacled bear *Tremarctos ornatus* (Mammalia : Carnivora : Ursidae) in Ecuador. Journal of Threatened Taxa 12:16204–16209.
- HALL, A. L. 2017. International spectacled bear studbook. Durrell Wildlife Conservation Trust. Jersey, New Jersey.
- HERNANI-LINEROS, L., E. GARCIA, AND L. F. PACHECO. 2020. Andean bear diet near to and far from a road. Ursus 31(e7):1–7.
- HERSHKOVITZ, P. 1957. On the possible occurrence of the spectacled bear, *Tremarctos ornatus* (F. Cuvier), in Panama. Saugtierkundliche Mitteilungen 5:122–123.
- HIRATA, Y. 1987. The Gigantopyramidal Agranular field in the cerebral cortices of the giant Panda (*Ailuropoda melanoleuca*) and the spectacled bear (*Tremarctos ornatus*). Pp. 135–142 in Proceedings of the Second International Symposium of Giant Panda. Tokio Zoological Park Society, Tokyo, Japan.
- HORNADAY, W. 1911. The spectacled bear. Zoological Society Bulletin 45:747–748.
- HORSFIELD, T. 1825. Description of the *Helarctos eurypilus*; exhibiting in the bear from the island of Borneo, the type of a subgenus of *Ursus*. Zoological Journal 2: 221-234
- JAMPEL, C. 2016. Cattle-based livelihoods, changes in the taskscape, and human-bear conflict in the Ecuadorian Andes. Geoforum 69:84–93.

- JIANGZUO, Q., AND J. J. FLYNN. 2020. The earliest ursine bear demonstrates the origin of plant-dominated omnivory in Carnivora. *ISCIENCE* 23:1–21.
- JORGENSON, J. P., AND S. SANDOVAL-A. 2005. Andean bear management needs and interactions with humans in Colombia. *Ursus* 16:108–116.
- KATTAN, G. ET AL. 2004. Range fragmentation in the spectacled bear *Tremarctos ornatus* in the northern Andes. *Oryx* 38:155–163.
- KITCHENER, A. C. 2010. Taxonomic issues in bears: Impacts on conservation in zoos and the wild, and gaps in current knowledge. *International Zoo Yearbook* 44:33–46.
- KLEINER, J. D., R. C. VAN HORN, J. E. SWENSON, AND S. M. J. G. STEYAERT. 2018. Rub-tree selection by Andean bears in the Peruvian dry forest. *Ursus* 29:58–66.
- KNAUF, T. ET AL. 2003. Comparative investigations on reproduction biology in different bear species - Anatomical, ultrasonographic and endocrine investigations. *Verhandlungsbericht uber Erkrankungen der Zootiere* 41:287–296.
- KRAUSE, J. ET AL. 2008. Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. *BMC Evolutionary Biology* 8.
- KUHME, W. 1991. Haltung und Fortpflanzung von Brillenbären (*Tremarctos ornatus*) im Kolner Zoo. *Der Zoologische Garten* 61:29–47.
- LARIVIERE, S. 2001. *Ursus americanus*. *Mammalian Species* 647:1–11.
- LENGWINAT, V. T., M. QUEST, F. GORITZ, W. TSCHERNER, AND L. KOLTER. 2001. Zur embryonalruhe des brillenbaren (*Tremarctos ornatus* Cuvier, 1825). *Der Zoologische Garten* 71:137–146.
- LESSON, R. 1827. *Manuel de Mammalogie, ou histoire naturelle des mamiferes.*, Roret, Libraire,

Paris. France.

LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Holmiae, Impensis Direct. Laurentii Salvii, Stockholm, Sweden.

LUZURIAGA, M. G. 2014. Estudio químico y parasitológico de muestras fecales del oso andino (*Tremarctos ornatus*) provenientes de 2 reservas ecológicas, 2 zoológicos y 1 centro de rescate en el Ecuador. Universidad San Francisco de Quito, Quito Ecuador.

MARÍA, A. 1924. *Tremarctos lasallei*. Boletín Sociedad Colombiana de Ciencias Naturales 13:113–118.

MÁRQUEZ, G., AND V. PACHECO. 2010. Nuevas evidencias de la presencia del Oso Andino (*Tremarctos ornatus*) en las Yungas de Puno, el registro más austral de Perú. *Revista Peruana de Biología* 17(3):377–380.

MARTÍNEZ, O., J. RECHBERGER, J. VEDIA-KENNEDY, AND M. THIBEAULT. 2008. Mamíferos medianos y grandes de la Serranía del Aguarague, Tarija (Bolivia). *Mastozoología Neotropical* 15:335–348.

MICHEL, G., K. ELZE, AND S. SEIFERT. 1983. Zur Enbyronalentwicklung des Baren unter besonderer beachtung des Baues der Plazenta. *Zoologische Garten* 53:290–294.

MINISTERIO DEL AMBIENTE Y AGUA DEL ECUADOR. 2020. Plan de acción para la conservación del oso andino (*Tremarctos ornatus*) en el Ecuador. Quito. Ecuador.

MINISTERIO DEL MEDIO AMBIENTE. 2001. Programa nacional para la conservación en Colombia del Oso Andino *Tremarctos ornatus*. Bogotá, Colombia.

MITCHELL, K. J. ET AL. 2016. Ancient mitochondrial DNA reveals convergent evolution of giant

- short-faced bears (Tremarctinae) in North and South America. *Biology Letters* 12:2–5.
- MOLINA, S., A. K. FULLER, D. J. MORIN, AND J. A. ROYLE. 2017. Use of spatial capture–recapture to estimate density of Andean bears in northern Ecuador. *Ursus* 28:117–126.
- MONDOLFI, E. 1971. El Oso Frontino (*Tremarctos ornatus*). *Defensa de la Naturaleza* 1:31–35.
- MONDOLFI, E. 1983. The feet and baculum of the spectacled bear , with comments on ursid phylogeny. *American Society of Mammalogists* 64:307–310.
- MONDOLFI, E. 1989. Notes on the distribution, habitat, food habits, status and conservation of the spectacled bear (*Tremarctos ornatus* Cuvier) in Venezuela. *Mammalia* 53:525–544.
- DEL MORAL, J. F., AND A. E. BRACHO. 2005. Evidence of Andean bear in northwest Argentina. *International Bear News* 14:31–32.
- DEL MORAL, J. F., AND A. E. BRACHO. 2009. Indicios indirectos de la presencia del oso andino (*Tremarctos ornatus* Cuvier, 1825) en el noroeste de Argentina. *Revista Museo Argentino de Ciencias Naturales* 11:69–76.
- MORRELL, N. 2018. Conservation planning at multiple scales : A density model and spatial planning tool to facilitate the conservation of Andean bears (*Tremarctos ornatus*) and the Northern Andes. The University of British Columbia, M.S. thesis. The University of British Columbia, Vancouver, Canada.
- NASH, W. G., AND S. J. O’BIEN. 1987. A comparative chromosome banding analysis of the ursidae and their relationship to other carnivores. *Cytogenetics and Cell Genetics* 45:206–212.
- NASSAR-MONTOYA, F. ET AL. 1997. Estudio Clínico del Oso de Anteojos (*Tremarctos ornatus*). P. 54 in *Investigación en el Parque 1994-1995*. Universidad de la Salle, Parque Jaime

Duque, Bogotá. Colombia.

NEWNHAM, R., AND W. DAVIDSON. 1966. Comparative study of the karyotypes of several species in Carnivora including the giant panda (*Ailuropoda melanoleuca*). *Cytogenetics* 5:152–163.

NEWNHAM, R., AND W. DAVIDSON. 1967. Authors addendum to: Comparative study of the karyotypes of several species in Carnivora, including the giant panda (*Ailutopoda melanoleuca*). *Cytogenetics* 6:156–157.

NICOLAU, A., K. LEMBERGER, M. MOSCA, A. LECLERC, A. LÉCU, AND D. PIN. 2018. Clinical and histopathological aspects of an alopecia syndrome in captive Andean bears (*Tremarctos ornatus*). *Veterinary Dermatology* 29:234-e85.

NOWAK, R. 1999. Walker's mammals of the world. Johns Hopkins University Press, Baltimore, Maryland.

OSGOOD, W. 1911. Mammals from western Venezuela and Eastern Colombia. *Field Museum of Natural History - Zoology* 10:33–66.

OTÁLORA-ARDILA, A. 2003. Mammals of the Oak Forest. *Acta Biológica Colombiana* 8:57–71.

OWEN, M., J. SHANKS, M. SUTHERLAND-SMITH, G. THOMAS, AND R. VAN HORN. 2009. Update on an investigation into a chronic skin disorder among captive Andean bears in North America. *International Bear News* 18:25–26.

PAISLEY, S. 2001. Andean bears and people in Apolobamba, Bolivia: Culture, conflict and conservation. Ph.D. dissertation, University of Kent, Canterbury, United Kingdom.

PAISLEY, S., AND D. L. GARSHELIS. 2006. Activity patterns and time budgets of Andean bears (*Tremarctos ornatus*) in the Apolobamba Range of Bolivia. *Journal of Zoology* 268:25–34.

PAISLEY, S., AND N. J. SAUNDERS. 2010. A god forsaken: The sacred bear in Andean iconography

- and cosmology. *World Archaeology* 42:245–260.
- PARRA-ROMERO, A., R. GALINDO-TARAZONA, J. F. GONZÁLEZ-MAYA, AND I. M. VELA-VARGAS. 2019. Not eating alone: Andean bear time patterns and potential social scavenging behaviors. *Therya* 10:49–53.
- PARQUES NACIONALES NATURALES DE COLOMBIA, AND WILDLIFE CONSERVATION SOCIETY. 2018. Estrategía para la conservación de oso andino en los Parques Nacionales Naturales de Colombia (2016-2031). Bogotá, Colombia.
- PEEL, R., J. PRICE, AND P. KARSTEN. 1979. Mother rearing of a spectacled bear cub *Tremarctos ornatus* at Calgary Zoo. *International Zoo Yearbook* 19:177–182.
- PÉREZ-TORRES, J. 2001. Guía para la conservación del oso andino y oso de anteojos *Tremarctos ornatus* (F.G. Cuvier, 1825). Convenio Andres Bello, Bogota, Colombia.
- PÉREZ MATA, A., H. GARCÍA PÉREZ, AND J. GAUTA PARRA. 2016. Morphological and molecular description of *Baylisascaris venezuelensis*, N. sp. from a natural infection in the South American spectacled bear *Tremarctos ornatus* Cuvier, 1825 in Venezuela. *Neotropical Helminthology* 10:85–103.
- PETERS, G., M. OWEN, AND L. ROGERS. 2007. Humming in bears: A peculiar sustained mammalian vocalization. *Acta Theriologica* 52:379–389.
- PEYTON, B. 1980. Ecology, distribution, and food habits of spectacled bears, *Tremarctos ornatus*, in Peru. *Journal of Mammalogy* 61:639–652.
- PEYTON, B. 1981. Spectacled bears in Peru. *ORYX* 16:48–56.
- PEYTON, B. 1987. Habitat components of the spectacled bear in Machu Picchu, Peru. *International Conference on Bear Research and Management* 7:127–133.

- PEYTON, B. 1999. Spectacled bear conservation action plan. P. 157–198 in Bears: status survey and conservation action plan (C. Servheen, S. Herrero, and B. Peyton, eds.) IUCN/SSC Bear Specialist group.
- PEYTON, B., E. YERENA, D. I. RUMIZ, J. P. JORGENSEN, AND J. OREJUELA. 1998. Status of wild Andean bears and policies for their management. *Ursus* 10:87–100.
- RAMSAY, E. 2003. Ursidae and Hyaenidae. *Zoo and Wild animal Medicine* (M. Fowler and E. Miller, eds.). Fifth ed. Saunders, St. Louis. Missouri.
- RECHBERGER, J., R. B. WALLACE, AND H. TICONA. 2001. Un movimiento de larga distancia de un oso andino (*Tremarctos ornatus*) en el norte del departamento de La Paz, Bolivia. *Ecología en Bolivia* 36:73–74.
- RÉYES, A. ET AL. 2018. Estructura y reproducción de la población de la población de osos andinos en el macizo de Chingaza, centro de la cordillera oriental colombiana. P. 227 in *Proceedings of the 25th Conference on Bear Research and Management* (S. Molina et al., eds.). Quito, Ecuador.
- RÉYES, A., D. RODRÍGUEZ, N. REYES-AMAYA, D. RODRÍGUEZ-CASTRO, H. RESTREPO, AND M. URQUIJO. 2017. Comparative efficiency of photographs and videos for individual identification of the Andean bear (*Tremarctos ornatus*) in camera trapping. *Therya* 8:83–87.
- RÍOS-UZEDA, B., H. GÓMEZ, AND R. B. WALLACE. 2006. Habitat preferences of the Andean bear (*Tremarctos ornatus*) in the Bolivian Andes. *Journal of Zoology* 268:271–278.
- RÍOS-UZEDA, B., H. GÓMEZ, AND R. B. WALLACE. 2007. A preliminary density estimate for Andean bear using camera-trapping methods. *Ursus* 18:124–128.
- RIVADENEIRA-CANEDO, C. 2008. Estudio del oso andino (*Tremarctos ornatus*) como dispersor

- legítimo de semillas y elementos de su dieta en la región de Apolobamba-Bolivia. *Ecología en Bolivia* 43:29–39.
- RODRIGUEZ, A., R. GOMEZ, A. MORENO, C. CUELLAR, AND D. J. LIZCANO. 2014. Record of a mountain tapir attacked by an Andean bear on a camera trap. *Tapir Conservation* 23:25–26.
- RODRÍGUEZ, D. ET AL. 2019a. Macizo Chingaza: Tierra de osos, tierra de gente, ¡tierra de todos! Empresa de Acueducto y Alcantarillado de Bogotá, Bogotá. Colombia.
- RODRÍGUEZ, D. ET AL. 2020. Andean bear (*Tremarctos ornatus*) population density and relative abundance at the buffer zone of the Chingaza National Natural Park , cordillera oriental of the Colombian andes. *Papéis Avulsos de Zoología* 60:1–7.
- RODRÍGUEZ, D., F. CUESTA, I. GOLDSTEIN, L. NARANJO, AND O. HERNÁNDEZ. 2003. Estrategia ecorregional para la conservación del oso andino - *Tremarctos ornatus*- en los Andes del norte.
- RODRÍGUEZ, D., A. RÉYES, AND S. GALLEGOS-SÁNCHEZ. 2019b. Northernmost distribution of the Andean bear (*Tremarctos ornatus*) in South America, and fragmentation of its associated Andean forest and Paramo ecosystems. *Therya* 10:161–170.
- RODRÍGUEZ, D., N. RÉYES, A. RÉYES, AND J. RODRÍGUEZ. 2013. Convenio de cooperación especial 200-12-17 Corporación Autónoma Regional CORPOGUAVIO - Y Fundacion para la Investigación, conservación y protección del Oso Andino - WII. Bogota, Colombia.
- RODRÍGUEZ-CLARK, K. M., AND A. SÁNCHEZ-MERCADO. 2006. Population management of threatened taxa in captivity within their natural ranges: Lessons from Andean bears (*Tremarctos ornatus*) in Venezuela. *Biological Conservation* 129:134–148.
- ROSENTHAL, M. A. 1987. International studbook for the spectacled bear *Tremarctos ornatus* (F.

- Cuvier, 1825).Lincoln Park Zoo, Chicago, Illinois.
- ROTH, H. 1964. Ein Beitrag zur Kenntnis von *Tremarctos ornatus* (Cuvier). Zoologische Garten 29:107–129.
- RUIZ-GARCIA, M. 2003. Molecular population genetic analysis of the spectacled bear (*Tremarctos ornatus*) in the northern Andean area. Hereditas 93:81–93.
- RUIZ-GARCÍA, M., J. Y. ARIAS-VÁSQUEZ, A. CASTELLANOS, L. KOLTER, AND J. M. SHOSTELL. 2020a. Molecular evolution (mitochondrial and nuclear microsatellites) in the Andean bear (*Tremarctos ornatus*: Ursidae, Carnivora): How many ESUs are there? Pp. 164–194 in Conservation genetics in mammals: Integrative research using novel approaches (J. Ortega and J. E. Maldonado, eds.). Springer International Publishing, New York.
- RUIZ-GARCÍA, M., J. Y. ARIAS-VÁSQUEZ, H. RESTREPO, C. H. CÁCERES-MARTÍNEZ, AND J. M. SHOSTELL. 2020b. The genetic structure of the spectacled bear (*Tremarctos ornatus*; Ursidae, Carnivora) in Colombia by means of mitochondrial and microsatellite markers. Journal of Mammalogy 101:1072-1090.
- RUIZ-GARCÍA, M., A. CASTELLANOS, J. Y. ARIAS-VÁSQUEZ, AND J. M. SHOSTELL. 2020c. Genetics of the Andean bear (*Tremarctos ornatus* ; Ursidae, Carnivora) in Ecuador: when the Andean Cordilleras are not an obstacle. Mitochondrial DNA Part A 31:190-208.
- RUIZ-GARCIA, M., P. OROZCO-TERWENGEL, E. PAYÁN, AND A. CASTELLANOS. 2003. Genética molecular de poblaciones aplicada al estudio de dos grandes carnívoros neotropicales (*Tremarctos ornatus* Cuvier, 1825- Oso Andino y *Panthera onca* Linné, 1758-Jaguar): lecciones de conservación. Bolentín de la Real Sociedad Española de Historia Natural 98:135–158.

- RUIZ GARCIA, M., P. OROZCO-TERWENGEL, A. CASTELLANOS, AND L. ARIAS. 2005. Microsatellite analysis of the spectacled bear (*Tremarctos ornatus*) across its range distribution. *Genes & Genetic Systems* 80:57–69.
- RUMIZ, D. I. ET AL. 2012. El ucumar (*Tremarctos ornatus*), mito y realidad de su presencia en la Argentina. *Mastozoología Neotropical* 19:359–366.
- SACCO, T., AND B. VAN VALKENBURGH. 2004. Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). *Journal of Zoology* 263:41–54.
- SALAZAR, J., AND S. ANDERSON. 1990. Informe sobre el estado actual del conocimiento del oso andino en Bolivia. *Ecología en Bolivia* 15:3–23.
- SALESA, M. J., G. SILICEO, M. ANTON, J. ABELLA, P. MONTOYA, AND J. MORALES. 2006. Anatomy of the “false thumb” of *Tremarctos ornatus* (Carnivora, Ursidae, Tremarctinae): Phylogenetic and functional implications. *Estudios Geológicos* 62:389–394.
- SANCHEZ-ARBOUIN, R., AND F. NASSAR-MONTOYA. 1997. Estudio reproductivo y congelación de semen del oso Andino (*Tremarctos ornatus*). P. 54 in *Investigación en el Parque 1994-1995*. Universidad de la Salle, Parque Jaime Duque, Bogotá, Colombia.
- SÁNCHEZ-MERCADO, A., J. R. FERRER-PARIS, S. GARCÍA-RANGEL, E. YERENA, B. A. ROBERTSON, AND K. M. RODRÍGUEZ-CLARK. 2014. Combining threat and occurrence models to predict potential ecological traps for Andean bears in the Cordillera de Mérida, Venezuela. *Animal Conservation* 17:388–398.
- SÁNCHEZ-MERCADO, A., J. R. FERRER-PARIS, E. YERENA, S. GARCÍA-RANGEL, AND K. M. RODRÍGUEZ-CLARK. 2008. Factors affecting poaching risk to vulnerable Andean bears *Tremarctos ornatus* in the Cordillera de Merida, Venezuela: space, parks and people. *Oryx*

42:437–447.

SAPORITI, E. 1949. Contribución al conocimiento de la biología del oso de lentos. *Anales de la Sociedad Científica Argentina* 147:3–12.

SCHAUL, J. 2006. *Baylisascaris transfuga* in captive and free-ranging population of bears (Family: Ursidae). Ph.D dissertation. The Ohio State University, Columbus.

SCHINZ, H. 1845. *Ursus fructilegus*. Systematisches verzeichniss aller bis jetzt bekannten Säugethiere, Vol. 1. Jent and Gassmann, Solothurn, Switzerland.

SCHÖNBAUER, S., S. KOLBL, AND A. SCHÖNBAUER-LANGLE. 1984. Perinatale staupeinfektion bei drei eisbaren (*Ursus maritimus*) und bei einem brülbaren (*Tremarctos ornatus*). Pp. 131–136 in Verhandlungsbericht des Internationalen symposiums über die Erkrankungen der Zootiere. Akademie-Verlag, Berlin, Germany.

SCLATER, P. L. 1868. Remarks upon a bear recently added to the Society's Menagerie (Plate VIII). *Proceedings of scientific meetings of the Zoological Society of London*:71–73.

SEAL, U. S., N. PHILLIPS, AND A. ERICKSON. 1970. Carnivora systematics: immunological relationships of bear serum albumins. *Comparative Biochemistry and Physiology* 32:33–48.

SEAL, U. S., W. SWAIM, AND A. ERICKSON. 1967. Hematology of the Ursidae. *Comparative Biochemistry and Physiology* 22:451–460.

SERFOR (SERVICIO NACIONAL FORESTAL Y DE FAUNA SILVESTRE). 2016. Plan nacional para la conservación del oso andino (*Tremarctos ornatus*) en el Perú: Periodo 2016-2026. Lima, Perú.

SERRANO-VILLAVICENCIO, J.E, BARTOLETTI T AND C. BUENO. 2020. Mammals collected by Johann Jakob von Tschudi during 1838-1842 for the *Muséum d'Historie Naturelle de*

- Neuchâtel*, Switzerland. Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais 15:905-931. DOI: <http://doi.org/10.46357/bcnaturais.v15i3.249>
- SOIBELZON, L. H., E. P. TONNI, AND M. BOND. 2005. The fossil record of South American short-faced bears (Ursidae, Tremarctinae). *Journal of South American Earth Sciences* 20:105–113.
- SOIBELZON, L., M. ROMERO, D. AGUILAR, AND V. TARTARINI. 2008. A Blancan (Pliocene) short-faced bear from El Salvador and its implications for tremarctines in South America. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 250:1–8.
- SOLARI, S., Y. MUÑOZ-SABA, J. V. RODRÍGUEZ-MAHECHA, T. R. DEFLER, H. E. RAMÍREZ-CHAVES, AND F. TRUJILLO. 2013. Riqueza, endemismo y conservación de los mamíferos de Colombia. *Mastozoología Neotropical* 20:301–365.
- SORIANO, P. J., A. D. DE PASCUAL, J. OCHOA G., AND M. AGUILERA. 1999. Biogeographic analysis of the mammal communities in the Venezuelan Andes. *Interciencia* 24:17–23.
- SPADY, T. J., D. G. LINDBURG, AND B. S. DURRANT. 2007. Evolution of reproductive seasonality in bears. *Mammal Review* 37:21–53.
- STAHL, P. W., AND J. S. ATHENS. 2001. A high elevation zooarchaeological assemblage from the northern Andes of Ecuador. *Journal of Field Archaeology* 21:161–176.
- STOCK, C. 1950. Bears from the pleistocene cave of San Josesito, Nuevo León, Mexico. *Journal of the Washington Academy of Sciences* 40:317–321.
- STUCCHI, M., AND J. FIGUEROA. 2013. Morfología cráneo–mandibular del oso andino *Tremarctos ornatus* (Carnivora: Ursidae). *Therya* 4:485–509.
- STUCCHI, M., R. SALAS-GISMONDI, P. BABY, J.-L. GUYOT, AND B. J. SHOCKEY. 2009. A 6,000+

- year-old specimen of a spectacled bear from an Andean cave in Peru. *Ursus* 20:63–68.
- SUAREZ, L. 1988. Seasonal distribution and food habits of spectacled bears *Tremarctos ornatus* in the highlands of Ecuador. *Studies on Neotropical Fauna and Environment* 23:133–136
- SÚAREZ, M. 1985. Hábitos alimenticios y distribución del oso de anteojos, *Tremarctos ornatus*, en el páramo suroriental del volcán Antisana, Ecuador. Pontificia Universidad Católica del Ecuador. Quito, Ecuador.
- TEDFORD, R.H, AND J. MARTIN. 2001. *Plionarctos*, a Tremarctine bear (Ursidae: Carnivora) from Western north America. *Journal of Vertebrate Paleontology* 21:311–32.
- THENIUS, V. E. 1976. Zur stammesgeschichtlichen Herkunft von *Tremarctos* (Ursidae, Mammalia). *Zeitschrift fur Säugetierkunde* 41:109–114.
- THOMAS, O. 1902. On the bear of Ecuador. *The Annals and Magazine of Natural History, including Zoology, Botany and Geology* 9:215–217.
- TIAN, Y., W. NIE, J. WANG, M. A. FERGUSON-SMITH, AND F. YANG. 2004. Chromosome evolution in bears: reconstructing phylogenetic relationships by cross-species chromosome painting. *Chromosome Research* 12:55–63.
- TIRIRA, D. G. 2009. Mamíferos ecuatorianos en museos de historia natural y colecciones científicas : 1 . El Museo de Historia Natural de Ginebra (Suiza). *Historia* 8:74–100.
- TRAJANO, E., AND H. FERRAREZZI. 1995. A fossil bear from northeastern Brazil , with a phylogenetic analysis of the South American extinct Tremarctinae (Ursidae). *Journal of Vertebrate Paleontology* 14:552–561.
- TROYA, V., F. CUESTA, AND M. PERALVO. 2004. Food habits of Andean bears in the Oyacachi River Basin, Ecuador. *Ursus* 15:57–60.

- TSCHUDI, J. 1844. *Ursus fugilegus*. Pp. 88–95 in *Untersuchungen über die Fauna Peruana* (J. Tschudi and J. L. Cabanis, eds.) Scheitlin and Zollikofer, St. Gallen, Switzerland.
- URREGO-CORREAL, G. 1990. Aguazuque. Evidencias de cazadores, recolectores y plantaciones en la altiplanicie de la cordillera oriental. Fundación de Investigaciones Arqueológicas Nacionales Banco de la República, Bogotá. Colombia.
- VAN HORN, R. C., M. SUTHERLAND-SMITH, A. E. BRACHO SARCOS, G. THOMAS, J. A. SHANKS, AND M. A. OWEN. 2019. The Andean bear alopecia syndrome may be caused by social housing. *Zoo Biology* 38:434–441.
- VAN HORN, R. C., B. ZUG, R. D. APPLETON, X. VELEZ-LIENDO, S. PAISLEY, AND C. LACOMBE. 2015. Photos provide information on age, but not kinship, of Andean bear. *PeerJ* 3:e1042.
- VAN HORN, R. C., B. ZUG, C. LACOMBE, X. VELEZ-LIENDO, AND S. PAISLEY. 2014a. Human visual identification of individual Andean bears *Tremarctos ornatus*. *Wildlife Biology* 20:291–299.
- VAN HORN, R., R. APPLETON, AND J. AMANZO. 2014b. Andean bears in two Peruvian forests are rarely photographed with meat. *International Bear News* 23:20–22.
- VARGAS, R. R., AND C. AZURDUY. 2006. Nuevos registros del Oso Andino (*Tremarctos ornatus*) en el departamento de Tarija, el registro más austral en Bolivia. *Mastozoología neotropical* 13:137–142.
- VELA-VARGAS, I. M., J. F. GONZÁLEZ-MAYA, A. PINEDA-GUERRERO, AND D. ZÁRRATE-CHARRY. 2014. Primer registro confirmado de Oso Andino (*Tremarctos ornatus*: Ursidae) en la Serranía de San Lucas, Bolívar, Colombia. *Mammalogy Notes* 1:11–12.
- VELEZ-LIENDO, X., F. ADRIAENSEN, AND E. MATTHYSEN. 2014. Landscape assessment of habitat

- suitability and connectivity for Andean bears in the Bolivian Tropical Andes. *Ursus* 25:172–187.
- VELEZ-LIENDO, X., AND S. GARCÍA-RANGEL. 2017. *Tremarctos ornatus* (errata version published in 2018). *The IUCN Red List of Threatened Species* 2017: e.T22066A123792952. <https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T22066A45034047.en>. Accessed on 11 March 2021.
- VITERI, M. P. 2007. Conservation genetics of Andean bears (*Tremarctos ornatus*) in northeastern Ecuador: molecular tools, genetic diversity and population size. M. S. thesis, University of Idaho, Moscow.
- VITERI, M. P., AND L. P. WAITS. 2009. Identifying polymorphic microsatellite loci for Andean bear research. *Ursus* 20:102–108.
- WEISSENGRUBER, G. E., G. FORSTENPOINTNER, A. KUBBER HEISS, K. RIEDELBERGER, H. SCHWAMMER, AND K. GANZBERGER. 2001. Occurrence and structure of epipharyngeal pouches in bears (Ursidae). *Journal of Anatomy* 198:309–314.
- WIENBERG, J. 2004. The evolution of the eutherian chromosomes. *Genomes and Evolution* 14:657–666.
- WILSON, D. E., AND D. M. REEDER. 2005. *Mammal species of the world. A taxonomic and geographic Reference*. 3rd Edition. Johns Hopkins University Press. Baltimore, Maryland.
- YERENA, E., AND D. TORRES. 1994. Spectacled bear conservation and dispersal corridors in Venezuela. *International Conference on Bear Research and Management* 9:169–172.
- YOUNG, K. 1990. Dispersal of *Styrax ovatus* seeds by the spectabled bear (*Tremarctos ornatus*). *Vida Silvestre Neotropical* 2:68–69.

YU, L., Y. W. LI, O. A. RYDER, AND Y. P. ZHANG. 2007. Analysis of complete mitochondrial genome sequences increases phylogenetic resolution of bears (Ursidae), a mammalian family that experienced rapid speciation. *BMC Evolutionary Biology* 7 198(2007).
<https://doi.org/10.1186/1471-2148-7-198>

ZAPATA-RÍOS, G., AND L. C. BRANCH. 2016. Altered activity patterns and reduced abundance of native mammals in sites with feral dogs in the high Andes. *Biological Conservation* 193:9–16.

ZAPATA-RÍOS, G., AND L. C. BRANCH. 2018. Mammalian carnivore occupancy is inversely related to presence of domestic dogs in the high Andes of Ecuador. *PLoS ONE* 13:e0192346.

ZHANG, B. ET AL. 2007. Genetic viability and population history of the giant panda, putting an end to the “evolutionary dead end”? *Molecular Biology and Evolution* 24:1801–1810.

ZUKOWSKI, B., AND A. ORMSBY. 2016. Andean bear livestock depredation and community perceptions in northern Ecuador. *Human Dimensions of Wildlife* 21:111–126.

Associate Editor was Robert K. Rose. Editor was Meredith J. Hamilton



Figure 2. Adult male *Tremarctos ornatus* in the Chingaza National Protected Area, Colombia, July 2016. Used with permission of the photographer, Luis Guillermo Linares-Romero.



Figure 3. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of an adult female *Tremarctos ornatus* from Nariño, Colombia (FNMH [Field Museum of Natural History] 88488. Photo used with permission of the Field Museum of Natural History, Chicago, Illinois. Condylbasal length is 193 mm.

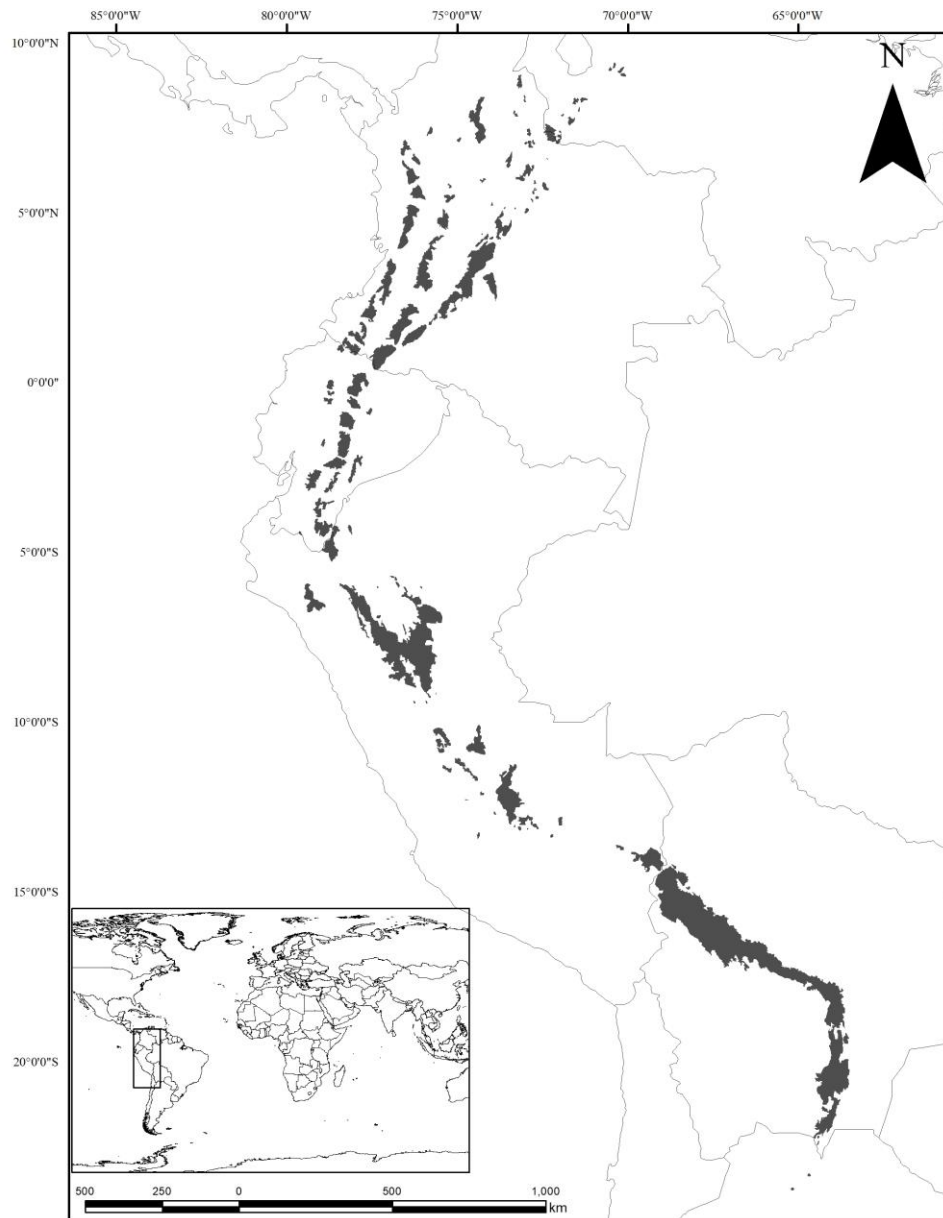


Figure 4. Distribution of *Tremarctos ornatus* based on Velez–Liendo and García-Rangel (2017).

APPENDIX 2.

When humans are gone: Andean bear occupancy patterns and effects from COVID-19 lockdown effects in the Chingaza Massif, Colombia.

I. Mauricio Vela-Vargas, Diego Lizcano, José F. González-Maya, John L. Koprowski

(Intended to submit to *Hystrix*)

When humans are gone: Andean bear occupancy patterns and effects from COVID-19 lockdown effects in the Chingaza Massif, Colombia.

I. MAURICIO VELA-VARGAS ^{a,b,c*}

^a School of Natural Resources and the Environment, ENR2 Bldg. 1064 E Lowell St., University of Arizona, Tucson, AZ, 85721, USA. imvelavargas@arizona.edu.

^b Wildlife Conservation Society – Colombia. Carrera 13 No. 77a-42, Bogotá, Colombia.

^c Proyecto de Conservación de Aguas y Tierras, ProCAT Colombia/International, Carrera 8 # 127c-36 Of. 101. Bogotá, Colombia. * Corresponding author

DIEGO LIZCANO ^d

^d Awake Travel. Transversal 8 No. 9-55, Cajicá, Colombia. dj.lizcano@gmail.com

JOSE F. GONZALEZ-MAYA ^{c,e}

^e Departamento de Ciencias Ambientales, DCBS, Universidad Autónoma Metropolitana-Lerma, Av. De las Garzas 10, El Panteón, 520056 Lerma, Estado de México, Mexico.

jfgonzalezmaya@gmail.com

^c Proyecto de Conservación de Aguas y Tierras, ProCAT Colombia/International, Carrera 8 # 127c-36 Of. 101. Bogotá, Colombia

JOHN L. KOPROWSKI ^{a,f}

^a School of Natural Resources and the Environment, ENR2 Bldg. 1064 E Lowell St., University of Arizona, Tucson, AZ, 85721, USA

^f Haub School of Environment and Natural Resources, University of Wyoming, 201 Bim Kendall House, Laramie, WY 82072, USA. jkoprows@uwyo.edu

Running head: Andean bear occupancy patterns in Colombia.

Abstract

The Chingaza Massif of Colombia is one of the most important cores areas for Andean bear (*Tremarctos ornatus*) conservation. This high-altitude complex includes the Chingaza National Natural Park that is not only crucial for Andean bear conservation, but the massif is also the principal source of water for Bogotá, the largest city and economic center of Colombia. The Andean bear is the only bear species distributed in South America. Despite being one of the most charismatic species in South America, many aspects of its biology and conservation status are understudied or unknown. Andean bears persist in heterogeneous landscapes moving between protected areas and associated buffer areas, but there is no available information on how this fragmented landscape of multiple uses affect the movements of the species. We conducted a camera-trapping study across the escarpment to assess the occupancy patterns of Andean bear at the Chingaza Massif. The study was performed during the COVID-19 lockdown established by the Colombian government, presenting a unique opportunity to assess occupancy in the absence of human activities at the Chingaza protected area and the massif. We use a Bayesian single-species occupancy framework to estimate occupancy as a function of landscape and anthropogenic factors. Our results showed that occupancy patterns were negatively affected by NDVI and positively affected by distance to towns. Detectability was affected negatively by the distance to human infrastructure. COVID-19 post-lockdown affected positively the occupancy increasing the areas that Andean bear used inside and outside of the Chingaza National Natural Park, potentially due to the decrease of human activities such as tourism, car movements decrease and absence of people in areas where the species is distributed. We discuss the application of random effects models to study occupancy patterns of elusive species across large

spatial scales. Our predictions provide the first comprehensive overview of Andean bear occupancy patterns in Colombia and share information with stakeholders and decision makers to focus conservation efforts for the species.

Introduction

The Andean bear (*Tremarctos ornatus*) is a species endemic to the tropical Andes region and is South America's only bear species (Vela-Vargas *et al.*, 2021b). The Andean bear is listed as Vulnerable (VU) globally according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Velez–Liendo and Garcia-Rangel, 2017) and in Colombia (Resolution 1912 of 2017). Despite being one of the most charismatic species in South America and considered an umbrella species, many aspects of its biology and population status are understudied or unknown (Crespo-Gascón and Guerrero-Casado, 2019; Garshelis, 2011). Lack of information presents obstacles for long-term management and conservation initiatives, and in Colombia, knowledge about the species is particularly scarce and is mostly comprised of distribution records (Rodríguez *et al.*, 2019; Vela-Vargas *et al.*, 2014), diet (Cáceres-Martínez *et al.*, 2020b), and human-Andean bear interactions (Escobar-Lasso *et al.*, 2020; Jorgenson and Sandoval, 2005; Parra-Romero *et al.*, 2019). Not until recently has there been studies of genetic structure (Ruiz-García *et al.*, 2020a, 2020b). For Andean bears, different countries have implemented monitoring programs to assess occupancy patterns and population dynamics, but in Colombia these programs are uncommon and have not been applied systematically (Acevedo *et al.*, 2019; Rodríguez-Castro *et al.*, 2015).

In Colombia, the Andean bear is distributed among highland ecosystems such Paramos and Cloud Andean Forest in the Andes Mountain Range (i.e., Andean region; Peyton, 1999; Vela-

Vargas *et al.*, 2021b) that cover approximately 25% of the country. Yet, these ecosystems are considered among the most transformed due to human development (and house 70% of Colombia population) and productive activities such as cattle grazing and agriculture (Armenteras *et al.*, 2011). For instance, natural Andean Forests and highland Paramos currently occupy less than 50% of their original distribution in Colombia (Llambí *et al.*, 2019). Habitat loss and fragmentation in mid to high elevations in Colombia's Andean region remain the primary threat to Andean bear persistence; available habitats have reduced by 15% between 1970–2015 (Cruz-Rodríguez *et al.*, 2020). Additionally, the increased frequency of negative human–Andean bear interactions has led to higher levels of mortality due to retaliatory illegal hunting (Jorgenson and Sandoval, 2005; Kattan *et al.*, 2004; Parra-Romero *et al.*, 2019).

The Colombian national plan for Andean bear conservation has prioritized *in situ* strategies for maintaining Andean bear population cores along the country and highlighted the need for generating information about population dynamics and ecological drivers of space use (Ministerio Del Medio Ambiente, 2001). However, studies on population dynamics of Andean bear populations, space use, and home range are scattered and have not been widespread nor replicated (Rodríguez *et al.*, 2020, 2021; Vela-Vargas *et al.*, 2021a). Most of the available information for the species in Colombia has been obtained through specific regional programs and independent research efforts and not from institutional systematic programs aimed at advancing the National plan (Hohbein *et al.*, 2021; Rodríguez-Castro *et al.*, 2015). In absence of such critical information, spatial dynamics data from other countries are often extrapolated as proxies (Castellanos, 2011; Molina *et al.*, 2017; Osterman *et al.*, 2021; Paisley, 2001), leaving the spatial ecology of the species in the fragmented landscapes of Colombia largely open to

speculation. Currently, Andean bears persist in heterogeneous landscapes moving between national protected areas boundaries and associated buffer areas, but there is no available information on how this fragmented, multiple use landscape affects bear movements (Garshelis, 2011; Sánchez-Mercado *et al.*, 2008).

One of the identified core areas for Andean bears conservation in Colombia is the Chingaza Massif (Ch-M), located within the eastern Andean range and includes Chingaza National Natural Park (Ch-NNP) (González-Maya *et al.*, 2017; Jorgenson and Sandoval, 2005). This high-altitude complex is not only crucial for the conservation of Andean bear, but the massif is also the principal source of water for Bogotá, Colombia's capital and largest city and economic center, and provides 80% of its water (Parques Nacionales Naturales de Colombia, 2016).

In this study, we assessed how natural landscape and anthropogenic variables influence occupancy patterns of Andean bears at the Ch-M in the eastern range of Colombia. We also assessed the potential effect of COVID-19 lockdowns on occupancy patterns. We predicted that higher occupancy inside the protected area than outside of it, with low occupancy areas driven by the anthropogenic factors such as roads and infrastructures, and positive occupancy response linked to COVID-19 lockdowns due to the lack of human disturbances.

Materials and methods

Study Area

The Chingaza Massif is located at the eastern Andes range of Colombia between Cundinamarca and Meta departments (states), with an area of 239.700 ha and 500 to 4.100 m elevation range (Vargas Rios and Pedraza 2004; González-Maya *et al.* 2017). At the core of the Massif is Chingaza National Natural Park (4° 20', - 73° 50'N and -73° 30', -73°55'W), with an area of

76.000 ha that maintains Andean Forest and Paramo ecosystems (Parra-Romero et al., 2019; Figure 1). A monomodal seasonal precipitation pattern occurs between May and August with rainfall averages between 1.200–4.500 mm/year, and average temperature between 6–7° Celsius (Morales Rivas *et al.*, 2007). For subsistence and cash income, rural communities along the massif are engaged in traditional high altitude agricultural, cattle ranching practices, and recently, ecotourism (Garavito González *et al.*, 2018; Pedraza *et al.*, 2020).

Figure 5.

Data collection

Due to heterogeneity of home ranges sizes among Andean bears (4.1–66.6 km²; Castellanos et al. 2005; Paisley and Garshelis 2006; Castellanos 2011, Vela-Vargas et al. 2021b), we followed Márquez et al., (2017) to apply a regular grid of 2 km² positioned inside and outside of the CH-NNP. Each grid cell represented approximately 1/3 of the mean home range size of females and the overlap of bear home range. We installed 81 camera traps (Bushnell® Trophy Cam Aggressor No-Glow) between September 2019 and October 2020 in Andean Forests and Páramo grasslands ecosystems in the Ch-M and preferred by Andean bears (Ríos-Uzeda et al. 2006). Camera traps were installed on trees at 60 cm above ground level. When trees were not available (e.g., paramos), we installed cameras on secured poles hidden from bears in areas deemed favorable to Andean bears and as close as possible to the grid center (Rovero and Zimmermann, 2016). We spaced cameras between 900 – 2000 meters to ensure independency, this range encompasses the difficult accessibility in the study area. Cameras operated nonstop and were programmed to take three successive photographs and 10-sec videos, with a 1-min delay between

subsequent triggers. No lures or baits were used as the aim was to capture natural behavior of the species.

Model Covariates

We aimed at evaluating the influence of multiple natural and anthropogenic covariates on detection and occupancy probabilities. We used a 30-m resolution digital elevation model extracted from Landsat 8-9 satellite (Kaita *et al.*, 2022) and derived landscape variables such as slope, altitude, aspect and normalized difference vegetation index (NDVI). Anthropogenic variables included Euclidian distance (m) to roads, towns, and human infrastructures inside of Ch-NNP. All variables were based on previous studies for the species (Hernani-Lineros *et al.*, 2020; Rojas-VeraPinto *et al.*, 2022; Zapata-Ríos and Branch, 2018).

For detection, we used camera effort, defined as the total number of days that camera traps effectively worked during the survey (Rovero and Zimmermann, 2016), distances to human structures in the Ch-NNP, and slope and aspect.

For occupancy, we again derived variables related to natural landscape features and human influence. These variables include the following: NDVI, distance to rivers, elevation, aspect, and slope, distances to roads, towns, and infrastructure inside the Ch-NNP.

We scaled covariates to have a mean of 0 and SD of 1 to allow direct comparison of models, a Spearman rank correlation analysis was performed among the co-variables to avoid autocorrelation, variables with high correlation ($|r| < 0.75$) were omitted from analyses.

Data Analysis

To model species occupancy, we used single-species, single-season occupancy models (Mackenzie *et al.*, 2018) implemented in a Bayesian framework using the *ubms* R package

(Kellner *et al.*, 2022). We selected that modeling framework due to the slow reproductive cycles of Andean bears (9-month interval between estrous cycles; Vela-Vargas *et al.*, 2021b), thus assuming a closed population during our sampling period. We fitted two occupancy models for Andean bears: 1) a fixed model that included landscape and human influence covariates as fixed effects, and 2) a random effect model which included the study site as a random effect to evaluate the effects of COVID-19 lockdowns during fieldwork (Bates *et al.*, 2015; Kellner *et al.*, 2022; Yackulic *et al.*, 2020). Detection histories were collapsed into multiple day sampling occasions to maximize detection estimates and improve likelihood convergence (Welsh *et al.*, 2013); we considered 7-d as a sampling period. To evaluate the effect of COVID-19 lockdowns during the sampling season, we included the effect of sites during the first 26 sampling occasions (pre-COVID-19 lockdowns) and the remaining sampling occasions after COVID lockdowns. For modelling purposes, we used four Markov chains of 100.000 iterations each and a burn-in period of 50.000 (Céspedes Arias *et al.*, 2022; Nguyen *et al.*, 2022). Model convergence was evaluated by R-hat statistics (≤ 1.1) and by visual examination of the trace plots (Céspedes Arias *et al.*, 2022; Gonçalves *et al.*, 2022; Kellner *et al.*, 2022; Nguyen *et al.*, 2022). Significance of the covariate effects was determined by the generation of 95% of intervals of the posterior distribution, if the coefficient of the 95% Bayesian credible interval did not overlap zero, was considered strong.

Occupancy models were compared using the leave-one-out cross-validation (LOO) method (Vehtari *et al.*, 2016). Based on LOO cross-validation, we used *ubms* to calculate the expected predictive accuracy (elpd; Kellner *et al.*, 2022). To evaluate model support relative the top model, pairwise differences were calculated for elpd (Δelpd) and its standard error (SE Δelpd).

We considered a model to show less support than the top model if the difference in elpd was greater than the standard error of that difference (Doll and Jacquemin, 2019).

Results

We obtained data from 66 of 81 camera trap stations, with a total sampling effort of 20.312 camera-trap days. Fifteen camera trap stations failed to provide data for various reasons (failure of the equipment, robbery). We obtained a total of 249 independent detections of Andean bear at the Ch-M.

We generated 36 fixed effects models of varying covariate combinations to evaluate Andean bear occupancy (Table 1). Covariates used were not correlated ($r < 0.5$). Fitted models outperformed the null model suggesting that covariables used in our research are adequate for evaluating Andean bear occupancy patterns.

Table 1.

The top model showed that Andean bears presented high occupancy levels ($\psi = 0.87 \pm 0.060$) along the Ch-M but low detectability ($p = 0.10 \pm 0.007$; Table 2). This model showed that NDVI values had a negative effect and increased distance to towns had a moderate positive effect on Andean bear occupancy (Figure 2). Detectability was explained by the decrease of distance to human infrastructure showing a moderate negative effect on detection of Andean bear at the Ch-M.

Table 2

Figure 7

The effect of COVID-19 lockdowns in Andean bear occupancy was positive, showing an increase in Andean bear occupancy during the lockdowns performed by the Colombian government during the pandemic (Table 3).

Table 3.

Andean bear predicted occupancy was similar between fixed and random models ($\psi=0.87$ and $\psi=0.71$), respectively. Differences in the predicted occupancy per pixel between the two models varied from 0.151 to -0.005 showing that predictions from the random effects model had higher accuracy in areas with medium and low occupancy (Figure 3).

Figure 7

Discussion

Evaluating presence or habitat use for elusive species such as the Andean bear can be challenging due to the complexity and accessibility of habitats used (Garshelis, 2011). Implementing occupancy modelling approaches provides reliable estimates to evaluate population status and inform management and conservation strategies (Castrillón-Hoyos *et al.*, 2023). Fixed and random effects models were congruent with other studies about occupancy of Andean bear, but our random effects model showed higher sensitivity in identifying medium and low occupancy areas; similar results have occurred with other elusive species (Nguyen *et al.*, 2022). Using random effects models increase the complexity and add additional model parameters to the analysis (Nguyen *et al.*, 2022). The decision of when and how researchers should apply this approach depends on the target species, data quality and quantity, and hypothesis of research.

We discuss below the implication of our findings on Andean bear management and conservation at the CH-M. To our knowledge, we are the first to evaluate COVID-19 pandemic effects on Andean bear populations in South America and apply structured occupancy patterns of the species in Colombia.

Andean bear occupancy patterns

Due to its ecological characteristics, *T. ornatus* have been designated as of excellent conservation value by Colombian authorities (Ministerio Del Medio Ambiente, 2001; Parques Nacionales Naturales de Colombia and Wildlife Conservation Society, 2018). To sustain long-term viable and healthy populations, monitoring programs must identify threats and areas where authorities should implement conservation actions (Hohbein and Nibbelink, 2021). Our results showed that occupancy patterns of Andean bear inside Chingaza National Park are high, given the status of a national protected area, but adjacent areas of Ch_NNP occupancy decreased given the presence of human activities such as cattle ranching and agriculture. This corroborates what has been reported among different regions of Colombia (Escobar-Lasso *et al.*, 2020; Gárrido Corredor *et al.*, 2021; Zárate Rodríguez *et al.*, 2022). The results are consistent with our hypothesis about the negative effect of human activities in areas that overlap with Andean bear range.

We identified landscape features that explained occupancy patterns across the Chingaza Massif of Colombia, and in doing so addressed a priority to understand the species habitat requirements across its distribution. The negative relationship of NDVI and occupancy is explained by the availability of highland ecosystems along the Ch-M such as paramos and shrublands. Andean bears are known to prefer highland ecosystems along its range (García-Rangel, 2012; Garshelis,

2022; Vela-Vargas *et al.*, 2021b) but given its dietary requirements and seasonal behaviors, the species uses multiple ecosystems (Cáceres-Martínez *et al.*, 2020a; Peyton, 1980; Ríos-Uzeda *et al.*, 2006). An apparent preference for less dense overstory canopies (i.e., lower NDVI values) could also be explained by high densities of *Miconia* spp trees, *Greigia* spp., *Puya* spp., *Espeletia* spp., and other preferred dietary items that normally are present in the Paramo and subparamo ecosystems present at the Ch-M. Highland ecosystems also usually maintain better natural cover that are less accessible by human communities (Elsen *et al.*, 2020).

As we hypothesized, proximity to human settlements negatively affected occupancy rates of Andean bears. Areas adjacent to Ch-NNP maintain high agriculture and livestock rates, diminishing availability and quality of natural habitat for the species and suggest that Andean bears avoid areas with higher disturbance of people and livestock activities (Aurich-Rodriguez *et al.*, 2022; Gárrido Corredor *et al.*, 2021; Parra-Romero *et al.*, 2019). In addition, being closer to human settlements have been a main predictor of human-Andean bear conflicts (Aurich-Rodriguez *et al.*, 2022; Rojas-VeraPinto *et al.*, 2022).

A surprising find was that detectability of the species is related to the proximity to human infrastructure. This could lead to bears moving outside of natural areas closer to human settlements. Bears being killed due to negative interactions have been reported in the Ch-M (Gárrido Corredor *et al.*, 2021; Parra-Romero *et al.*, 2019) and send alarms to authorities to generate actions to practice sustainable tourism practices for Andean bears.

COVID-19 lockdown effects on occupancy of Andean bears

To stop or slow COVID-19 transmission rates, Colombian government declared a total lockdown from March 25 to August 31 of 2020. With the decrease of human traffic or “anthropause”

(Blount *et al.*, 2021; Rutz *et al.*, 2020), we present the first report of how Andean bear occupancy patterns were affected by the COVID-19 pandemic. Our results showed a positive effect after lockdown in Colombia, suggesting that occupancy increased during lockdowns in Colombia. Decreases in human activities during the COVID-19 pandemic have affected bear behaviors and space use globally. For example, black bear (*Ursus americanus*) exhibited increased detection rates due to the decrease of motorized vehicle activities in adjacent locations of protected areas in Canada (Procko *et al.*, 2022), and brown bears (*Ursus arctos*) expanded into rarely used spaces when humans were present in Italy (Corradini *et al.*, 2021). In Colombia, records of Andean bears close to human settlements in areas where the species was normally absent were made and transmitted in the popular news.

We found that COVID-19 post-lockdowns at the Chingaza massif is positively related with the occupancy of Andean bears ($\sigma = 1.48$). This positive relationship could be explained by the decrease of visitors to the protected area and its surroundings, diminishing disturbance activities of tourism and thus promoting movements in landscapes that bears did not normally use.

Conservation implications

Our work presented the occupancy dynamics of *T. ornatus* at the eastern range of Colombia. Specifically, we show the importance of how protected areas should connect conservation work in adjacent areas outside of its boundaries. This provides useful information to inform management actions for the species inside and outside of protected areas in Colombia. Our results can be used to prioritize areas outside of protected areas to work in conservation activities and manage pressures to highland Andean ecosystems, improving productive activities around protected areas reconciling production and conservation. Management of cattle

production is priority to avoid the introduction of infectious diseases into the population of Andean bear at the Ch-M and diminishing negative human – Andean bear interactions (Aurich-Rodriguez *et al.*, 2022; Rojas-VeraPinto *et al.*, 2022, Quintero *et al.* 2023)

The anthropause showed that human activities can lead to ecological disasters, but also generated a question about how to face the challenge of conserve wildlife while promoting responsible recreation activities. How the pandemic affected biodiversity globally? Is to early to answer this main question and will be a main subject of research for several years, but our research showed a small portion of this answer. Globally in protected areas, COVID-19 pandemic forced to closures and reduced the stress on sensitive biological groups. These effects were temporary, but forced to managers, researchers, and the society in general to take new actions in conservation sciences.

With our results we provide the first report of how Andean bears occupancy patterns were affected by the COVID-19 pandemic in Colombia and South America and offer a base line to evaluate the real effect of human activities on a flagship species like Andean bears.

Acknowledgments

Thanks to the rangers of Chingaza National Natural Protected Area, especially to Oscar Raigozo and Julian Zamora for their companionship and help in the camera trap installation, frequent checks, and removal process. To Juan Camilo Rubiano, Camilo Paredes and Fernando Alvarez, Giacomo Cremonesi, Neil Dutt, and Jan Schipper for their effort in the field, long hikes, and company in the data collection process. To the Chingaza National Natural Park Director Juan Carlos Clavijo for his support on the project. IMV-V acknowledges for the support provided by the COLCIENCIAS-Fulbright program in Colombia, the College of Agriculture and Life Science of the University of Arizona and an anonymous donor's support. Thanks to the Arizona Center

for Nature Conservation – Phoenix Zoo and Reid Zoo Park for their support throughout the project. To WCS Colombia staff for its support during the field data collection.

Bibliography

- Acevedo, C., Celis, J., Cuevas, D., Giraldo, M., Lievano, I., Marquez, R., Maya, A.M., Parra, N., Rincon, L., Roncancio, N., Salazar, M., Silva, F., Troncoso, J.C., Villegas, M.C. 2019. Conservamos la Vida : Patrones de ocupación y diagnóstico de paisaje de conflicto entre el oso andino y la gente en la Unidad Núcleo de Conservación Tatamá - Farallones - Munchique. Andean Bear Conservation Aliance, Cali.
- Armenteras, D., Rodríguez, N., Retana, J., Morales, M. 2011. Understanding deforestation in montane and lowland forests of the Colombian Andes. *Reg Environ Change* 11(3): 693–705. doi:10.1007/s10113-010-0200-y.
- Aurich-Rodriguez, F., Piana, R.P., Appleton, R.D., Burton, A.C. 2022. Threatened Andean bears are negatively affected by human disturbance and free-ranging cattle in a protected area in northwest Peru. *Mamm. Biol.* 102(1): 177–187. doi:10.1007/s42991-021-00217-z.
- Bates, D., Mächler, M., Bolker, B.M., Walker, S.C. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1). doi:10.18637/jss.v067.i01.
- Blount, J.D., Chynoweth, M.W., Green, A.M., Şekercioğlu, Ç.H. 2021. Review: COVID-19 highlights the importance of camera traps for wildlife conservation research and management. *Biol Conserv* 256. doi:10.1016/j.biocon.2021.108984.
- Cáceres-Martínez, C.H., Rivera-Torres, C.Y., López-Orjuela, H.A., Zamora-Abrego, J.G., González-Maya, J.F. 2020a. Viviendo en los Andes: registros notables de la distribución altitudinal del oso

- andino, *Tremarctos ornatus* (Ursidae) en Boyacá, Colombia. *Arx Misc Zool* 18: 161–171.
doi:10.32800/amz.2020.18.0161.
- Cáceres-Martínez, C.H., Sánchez Montano, L.R., Acevedo, A.A., González-Maya, J.F. 2020b. Diet of Andean bears in Tamá National Natural Park , Colombia. *Ursus* 31(e10): 1–11.
doi:10.2192/URSUS-D-18-00006.1.
- Castellanos, A. 2011. Andean bear home ranges in the Intag region, Ecuador. *Ursus* 22(1): 65–73.
doi:10.2192/URSUS-D-10-00006.1.
- Castrillón-Hoyos, L., Rincón, L., Troncoso-Saavedra, J., Giraldo-Rojas, M., Hernández-Rincón, J., Velásquez-Vázquez, A., Gallego-López, L., Guzmán-Valencia, C., Gallego-Patiño, L., Rojas-Osorio, J., Gómez-González, J., Osorio-Parra, L., Marquez, R., Bianchi, G., Goldstein, I., Márquez, R. 2023. Occupancy and habitat use by the Andean bear are negatively affected by human presence and forest loss. *J Nat Conserv* 73: 126409. doi:10.1016/j.jnc.2023.126409.
- Céspedes Arias, L.N., Wilson, S., Bayly, N.J. 2022. Community modeling reveals the importance of elevation and land cover in shaping migratory bird abundance in the Andes. *Ecol. Appl.* 32(1):e02481.10.1002/eap.2481.
- Corradini, A., Peters, W., Pedrotti, L., Hebblewhite, M., Bragalanti, N., Tattoni, C., Ciolli, M., Cagnacci, F. 2021. Animal movements occurring during COVID-19 lockdown were predicted by connectivity models. *Glob Ecol Conserv* 32. doi:10.1016/j.gecco.2021.e01895.
- Crespo-Gascón, S., Guerrero-Casado, J. 2019. The role of the spectacled bear (*Tremarctos ornatus*) as an umbrella species for Andean ecoregions. *Wildl. Res.* 46(2): 176–183. doi:10.1071/wr18056.
- Cruz-Rodríguez, C., Reyes, A., Parra-Romero, A., Cáceres-Martínez, C.H., Rodríguez, D., Lizcano, D., Zárrate-Charry, D., Restrepo, H., Gómez, I., Aconcha-Abril, I., Vela-Vargas, I.M., González-

- Maya, J.F., Nova Leon, L., Olaya-Herrera, H., Reyes-Amaya, N., Pulido-Santacruz, P., Marquez, R., Noguera-Urbano, E. 2020. El oso andino. Impactos de las acciones humanas sobre su distribución. In: Moreno, L.A., Andrade, G.I., Didier, G., Hernandez-Manrique, O.(Eds.) Biodiversidad 2020. Estado y tendencias de la biodiversidad continental de Colombia. . Instituto de Investigación de Recursos Biológicos Alexander von Humboldt , Bogotá, D.C. .
- Doll, J.C., Jacquemin, S.J. 2019. Bayesian model selection in fisheries management and ecology. *Journal of Fish and Wildlife Management*, U.S. Fish and Wildlife Service: 691–707 p.
- Elsen, P.R., Monahan, W.B., Merenlender, A.M. 2020. Topography and human pressure in mountain ranges alter expected species responses to climate change. *Nature Commun* 11(1). doi:10.1038/s41467-020-15881-x.
- Escobar-Lasso, S., Cepeda-Duque, J., Gil-Fernandez, M., González-Maya, J.F. 2020. Is the banana ripe? - Andean bear-human conflict in a protected area of Colombia. *Hum. – Wildl. Interact.* 14(2): 1–17.
- Garavito González, L., Gómez Zárate, D.P., Palacio Tamayo, D. 2018. Gobernanza territorial en los páramos Chingaza y Sumapaz-Cruz Verde. Una comparación de sus principales actores y problemáticas. *Perspectiva Geográfica* 23(1): 11–30. doi:10.19053/01233769.6703.
- García-Rangel, S. 2012. Andean bear *Tremarctos ornatus* natural history and conservation. *Mamm Rev* 42(2): 85–119. doi:10.1111/j.1365-2907.2011.00207.x.
- Gárrido Corredor, A.M., Cottyn, H., Martínez-Medina, S., Wheatley, C., Sánchez, A., Kirshner, J., Cowie, H., Touza-Montero, J., White, P.C.L. 2021. Oso , Osito ¿ a Qué Venís? Andean Bear Conflict , Conservation , and Campesinos in the Colombian Páramos. *Sustainability* 13(104889): 1–18. doi:https://doi.org/10.3390/ su131910489.

- Garshelis, D.L. 2011. Andean bear density and abundance estimates — How reliable and useful are they? *Ursus* 22(1): 47–64. doi:10.2192/URSUS-D-10-00030.1.
- Garshelis, D.L. 2022. Understanding Species–Habitat Associations: A Case Study with the World’s Bears. *Land* 11(2): 180. <https://doi.org/10.3390/land11020180>.
- Gonçalves, A.L.S., de Oliveira, T.G., Arévalo-Sandi, A.R., Canto, L. V., Yabe, T., Spironello, W.R. 2022. Composition of terrestrial mammal assemblages and their habitat use in unflooded and flooded blackwater forests in the Central Amazon. *PeerJ* 10. doi:10.7717/peerj.14374.
- González-Maya, J.F., Galindo-Tarazona, R., Urquijo-Collazos, M.M., Zárate-Vanegas, M., Parra-Romero, A. 2017. *El Oso Andino en el Macizo de Chingaza*. Bogotá, Colombia.
- Hernani-Lineros, L., Garcia, E., Pacheco, L.F. 2020. Andean bear diet near to and far from a road. *Ursus* 31(e7): 1–7. doi:10.2192/URSUS-D-19-0003.1.
- Hohbein, R.R., Nibbelink, N.P. 2021. Omnidirectional connectivity for the Andean bear (*Tremarctos ornatus*) across the Colombian Andes. *Landsc Ecol* 36(11): 3169–3185. doi:10.1007/s10980-021-01299-3.
- Hohbein, R.R., Nibbelink, N., Cooper, R.J. 2021. Impacts of decentralized environmental governance on Andean Bear conservation in Colombia. *Environ Manage* 68(6): 882–899. doi:10.1007/s00267-021-01532-4.
- Jorgenson, J.P., Sandoval, A.S. 2005. Andean bear management needs and interactions with humans in Colombia. *Ursus* 16: 108–116.
- Kaita, E., Markham, B., Haque, M.O., Dichmann, D., Gerace, A., Leigh, L., Good, S., Schmidt, M., Crawford, C.J. 2022. Landsat 9 Cross Calibration Under-Fly of Landsat 8: Planning, and Execution. *Remote Sens (Basel)* 14(21). doi:10.3390/rs14215414.

- Kattan, G., Hernández, O.L., Goldstein, I., Rojas, V., Murillo, O., Gómez, C., Restrepo, H., Cuesta, F. 2004. Range fragmentation in the spectacled bear *Tremarctos ornatus* in the northern Andes. *Oryx* 38(02): 155–163. doi:10.1017/S0030605304000298.
- Kellner, K.F., Fowler, N.L., Petroelje, T.R., Kautz, T.M., Beyer, D.E., Belant, J.L. 2022. ubms: An R package for fitting hierarchical occupancy and N-mixture abundance models in a Bayesian framework. *Methods Ecol Evol* 13(3): 577–584. doi:10.1111/2041-210X.13777.
- Llambí, L.D., Becerra, M.T., Peralvo, M., Avella, A., Baruffol, M., Flores, L.J. 2019. Monitoring biodiversity and ecosystem services in Colombia’s high Andean ecosystems: Toward an integrated strategy. *Mt Res Dev* 39(3): A8–A20. doi:10.1659/MRD-JOURNAL-D-19-00020.1.
- Mackenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E. 2018. *Occupancy estimation and modelling: Inferring patterns and dynamics of species occurrence*. Second Edition, Academic Press, London.
- Márquez, R., Bianchi, G., Isasi-Catalá, E., Gutiérrez, V.R., Goldstein, I. 2017. *Guía para el Monitoreo de la Ocupación de Oso Andino*. Wildlife Conservation Society. Andean Bear Conservation Alliance. 58p.
- Ministerio Del Medio Ambiente. 2001. *Programa nacional para la conservación en Colombia del Oso Andino Tremarctos ornatus*.: 28 p. Bogotá, Colombia.
- Molina, S., Fuller, A.K., Morin, D.J., Royle, J.A. 2017. Use of spatial capture–recapture to estimate density of Andean bears in northern Ecuador. *Ursus* 28(1): 117–126. doi:10.2192/ursu-d-16-00030.1.
- Morales Rivas, M., Otero García, J., van der Hammen, T., Perdigón, A., Cadena Vargas, C., Pedraza Peñaloza, C., Rodríguez Eraso, N., Franco Aguilera, C., Betancourth Suárez, J., Olaya Ospina,

- E., Posada Gillede, E., Cárdenas Valencia, L. 2007. Atlas de páramos de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia.
- Nguyen, T. V., Wilting, A., Niedballa, J., Nguyen, A., Rawson, B.M., Nguyen, A.Q.H., Cao, T.T., Wearn, O.R., Dao, A.C., Tilker, A. 2022. Getting the big picture: Landscape-scale occupancy patterns of two Annamite endemics among multiple protected areas. *Conserv Sci Pract* 4(3): e620. doi:10.1111/csp2.620.
- Osterman, W.H.A., Cornejo, F.M., Osterman, J. 2021. An Andean bear population hotspot in Northern Peru. *Ursus* 2021(32e12). doi:10.2192/ursus-d-20-00005.3.
- Paisley, S. 2001. Andean bears and people in Apolobamba, Bolivia: Culture, conflict and conservation. Ph.D Dissertation. Durrell Institute of Conservation and Ecology. University of Kent. Canterbury, United Kingdom.
- Parques Nacionales Naturales de Colombia. 2016. Reformulacion Participativa Del Plan De Manejo Parque Nacional Natural Chingaza.: 273 p. Bogotá, Colombia.
- Parques Nacionales Naturales de Colombia, Wildlife Conservation Society. 2018. Estrategia para la conservación del oso andino en los Parques Nacionales Naturales de Colombia (2016-2031).: 31 p. Bogotá D.C.
- Parra-Romero, A., Galindo-Tarazona, R., González-Maya, J.F., Vela-Vargas, I.M. 2019. Not eating alone : Andean bear time patterns and potential social scavenging behaviors. *Therya* 10(1): 49–53. doi:10.12933/therya-19-625.
- Pedraza, S., Sanchez, A., Clerici, N., Ospina, L., Quintero, A., Escobedo, F.J. 2020. Perception of conservation strategies and nature’s contributions to people around Chingaza National Natural Park, Colombia. *Environ Conserv* 47(3): 158–165. doi:10.1017/S037689292000020X.

- Peyton, B. 1980. Ecology, distribution, and food habits of spectacled bears, *Tremarctos ornatus*, in Peru. *J Mammal* 61(4): 639–652. doi:10.1644/870.1.Key.
- Peyton, B. 1999. Spectacled bear conservation action plan. In: Servheen, C., Herrero, S., Peyton, B.(Eds.) *Bears: status survey and conservation action plan*. 157–198.
- Procko, M., Naidoo, R., LeMay, V., Burton, A.C. 2022. Human impacts on mammals in and around a protected area before, during, and after COVID-19 lockdowns. *Conserv Sci Pract* 4(7). doi:10.1111/csp2.12743.
- Ríos-Uzeda, B., Gómez, H., Wallace, R.B., Rios-Uzeda, B., Gomez, H., Wallace, R.B. 2006. Habitat preferences of the Andean bear (*Tremarctos ornatus*) in the Bolivian Andes. *J Zool* 268(3): 271–278. doi:10.1111/j.1469-7998.2005.00013.x.
- Rodríguez, D., Reyes, A., Quiñones-guerrero, A., Poveda-Gómez, F.E., Castillo-Navarro, Y., Duque, R., Reyes-Amaya, N. 2020. Andean bear (*Tremarctos ornatus*) population density and relative abundance at the buffer zone of the Chingaza National Natural Park , Cordillera Oriental of the Colombian Andes. *Pap Avulsos Zool* 60(e20206030): 1–7. doi:10.11606/1807-0205/2020.60.30.
- Rodríguez, D., Reyes, A., Reyes-Amaya, N., Gallegos-Sánchez, S., Gutierrez, J., Suárez, R., Prieto, F. 2019. Northernmost distribution of the Andean bear (*Tremarctos ornatus*) in South America, and fragmentation of its associated andean forest and paramo ecosystems. *Therya* 10(2): 161–170. doi:10.12933/therya-19-756.
- Rodríguez, D., Reyes, A., Tarquino-Carbonel, A. del P., Restrepo, H., Reyes-Amaya, N. 2021. Space use by a male Andean bear (*Tremarctos ornatus*) tracked with GPS telemetry in the Macizo Chingaza, Cordillera Oriental of the Colombian Andes. *Notas sobre Mamíferos Sudamericanos* 03(1): 001–008. doi:10.31687/saremnms.21.2.4.

- Rodríguez-Castro, D., Contento, S., Grajales, D., Rodríguez, D. 2015. Evaluación del estado de aplicación del Programa Nacional para la Conservación en Colombia del Oso Andino (*Tremarctos ornatus*). Rev Biodivers Neotrop 5(1): 36–46.
- Rojas-VeraPinto, R., Bautista, C., Selva, N. 2022. Living high and aty risk: predicting Andean bear occurrence and conflicts with humans in southeastern Peru. Glob Ecol Conserv 36: e02112. doi:10.1016/j.gecco.2022.e02112.
- Rovero, F., Zimmermann, F. 2016. Camera trapping for wildlife research. Rovero, F., Zimmermann, F.(Eds.), Pelagic Publishing , Exeter.
- Ruiz-García, M., Arias-Vásquez, J.Y., Castellanos, A., Kolter, L., Shostell, J.M. 2020a. Molecular evolution (mitochondrial and nuclear microsatellites) in the Andean bear (*Tremarctos ornatus*: Ursidae, Carnivora): How many ESUs are there? In: Ortega, J., Maldonado, J.E.(Eds.) Conservation genetics in mammals: Integrative research using novel approaches. Springer International Publishing, New York. 164–194.
- Ruiz-García, M., Vásquez, J.Y.A., Restrepo, H., Cáceres-Martínez, C.H., Shostell, J.M. 2020b. The genetic structure of the spectacled bear (*Tremarctos ornatus*; Ursidae, Carnivora) in Colombia by means of mitochondrial and microsatellite markers. J Mammal 101(4): 1072–1090. doi:10.1093/jmammal/gyaa082.
- Rutz, C., Loretto, M.C., Bates, A.E., Davidson, S.C., Duarte, C.M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T., Primack, R.B., Ropert-Coudert, Y., Tucker, M.A., Wikelski, M., Cagnacci, F. 2020. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. Nature Ecology and Evolution, Nature Research: 1156–1159 p.

- Sánchez-Mercado, A., Ferrer-Paris, J.R., Yerena, E., García-Rangel, S., Rodríguez-Clark, K.M. 2008. Factors affecting poaching risk to vulnerable Andean bears *Tremarctos ornatus* in the Cordillera de Merida, Venezuela: space, parks and people. *Oryx* 42(3): 437–447. doi:10.1017/S0030605308006996.
- Shannon, G., Lewis, J.S., Gerber, B.D. 2014. Recommended survey designs for occupancy modelling using motion-activated cameras: insights from empirical wildlife data. *PeerJ* 2: e532. doi:10.7717/peerj.532.
- Vargas Rios, O., Pedraza, P. 2004a. Parque Nacional Natural Chingaza. Gente Nueva Era Editorial, Bogotá, Colombia.
- Vargas Rios, O., Pedraza, P. 2004b. Parque Nacional Natural Chingaza. Gente Nueva Era Editorial, Bogotá, Colombia.
- Vehtari, A., Gelman, A., Gabry, J. 2016. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat Comput* 27(5): 1413–1432. doi:10.1007/s11222-016-9696-4.
- Vela-Vargas, I.M., Clavijo, J.C., Raigozo, O., Zamora, J., Arias-Bernal, L., Koprowski, J.L. 2021a. Novel insights into Andean bear home range in the Chingaza Massif, Colombia. *International Bear News* 30(1): 28–30.
- Vela-Vargas, I.M., González-Maya, J.F., Pineda-Guerrero, A., Zárrate-Charry, D. 2014. Primer registro confirmado de Oso Andino (*Tremarctos ornatus*: Ursidae) en la Serranía de San Lucas, Bolívar, Colombia. *Mammalogy Notes* 1(1): 11–12.
- Vela-Vargas, I.M., Jorgenson, J.P., González-Maya, J.F., Koprowski, J.L. 2021b. *Tremarctos ornatus* (Carnivora: Ursidae). *Mammalian Species* 53(1006): 78–94. doi:10.1093/mspecies/seab008.

- Velez-Liendo, X., Garcia-Rangel, S. 2017. *Tremarctos ornatus*. *Tremarctos ornatus* (errata version published in 2018). The IUCN Red List of Threatened Species 2017: e.T22066A123792952. <http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T22066A45034047.en>
- Welsh, A.H., Lindenmayer, D.B., Donnelly, C.F. 2013. Fitting and interpreting occupancy models. *PLoS One* 8(1). doi:10.1371/journal.pone.0052015.
- Yackulic, C.B., Dodrill, M., Dzul, M., Sanderlin, J.S., Reid, J.A. 2020. A need for speed in Bayesian population models: a practical guide to marginalizing and recovering discrete latent states. *Ecological Applications* 30(5). doi:10.1002/eap.2112.
- Zapata-Ríos, G., Branch, L.C. 2018. Mammalian carnivore occupancy is inversely related to presence of domestic dogs in the high Andes of Ecuador. *PLoS One* 13(2): e0192346. doi:10.1371/journal.pone.0192346.
- Zárate Rodríguez, P.T., Collazos-Escobar, L.F., Benavides-Montaña, J.A. 2022. Endoparasites infecting domestic animals and spectacled sears (*Tremarctos ornatus*) in the rural high mountains of Colombia. *Vet Sci* 9(10). doi:10.3390/vetsci9100537.

List of Tables

Table 1. Model selection for occupancy of Andean bear (*Tremarctos ornatus*) at the Chingaza Massif, Colombia. The top 5 models were ranked with the expected predictive accuracy predictor (elpd). Δelpd represents the differences in elpd. ΔSE is the standard error of Δelpd and weight of each variable influencing the parameter of the models. Andean bear Occupancy (ψ) and detectability (p) parameters are indicated.

Variable abbreviations include DI: Euclidean Distance to human infrastructures, NDVI: Normalized Difference Vegetation Index, DT: Euclidean Distance to Towns, DRi: Euclidean distance to rivers, Dro: Euclidean distance to Roads.

Model	elpd	Δelpd	ΔSE	Weight	$\psi \pm \text{SD}$	$p \pm \text{SD}$
$p(\text{DI})\psi(\text{NDVI}+\text{DT})$	-832.15	0.00	0.00	0.34	0.87±0.06	0.10±0.0
$p(\text{DI})\psi(\text{DT}+\text{NDVI}+\text{DRi})$	-833.01	0.85	0.42	0.00	--	--
$p(\text{DI})\psi(\text{DT}+\text{NDVI}+\text{DRo})$	-833.08	0.92	1.07	0.20	--	--
$p(\text{DI})\psi(\text{NDVI})$	-833.39	1.12	2.72	0.083	--	--
$p(\text{DI})\psi(\text{DT}+\text{NDVI}+\text{DRo}+\text{DRi})$	-834.115	1.95	1.17	0.000	--	--

Table 2. Fixed effects model for Andean bear (*Tremarctos ornatus*) occupancy in the Chingaza Massif. DI: Euclidean Distance to human infrastructures, NDVI: Normalized Difference Vegetation Index, DT: Euclidean Distance to Towns.

Parameter	Covariable	Coefficient	SE	CI Lower	CI Upper
ψ 0.87 ± 0.06	Intercept	1.91	0.53	1.02	3.10
	DT	0.86	0.42	0.09	1.76
	NDVI	-1.02	0.44	-1.96	-0.24
p 0.10 ± 0.007	Intercept	-2.23	0.07	-2.37	-2.09
	DI	-0.27	0.07	-0.41	-0.12

Table 3. Random effects model for occupancy of Andean bear (*Tremarctos ornatus*) at the Chingaza Massif, Colombia. Variables used were DI: Euclidean Distance to human infrastructures (m), NDVI: Normalized Difference Vegetation Index, DT: Euclidean Distance to Towns.

Parameter	Covariable	Coefficient	SE	CI Lower	CI Upper
ψ 0.87 ± 0.06	Intercept	1.09	0.43	0.39	2.11
	DT	0.74	0.39	0.04	1.61
	NDVI	-1.83	0.41	-1.77	-0.13
	σ (1 Site)	1.48	0.79	0.22	3.24
p 0.10 ± 0.007	Intercept	-1.94	0.07	-2.10	-1.79
	DI	-0.22	0.07	-0.38	-0.07

List of Figures

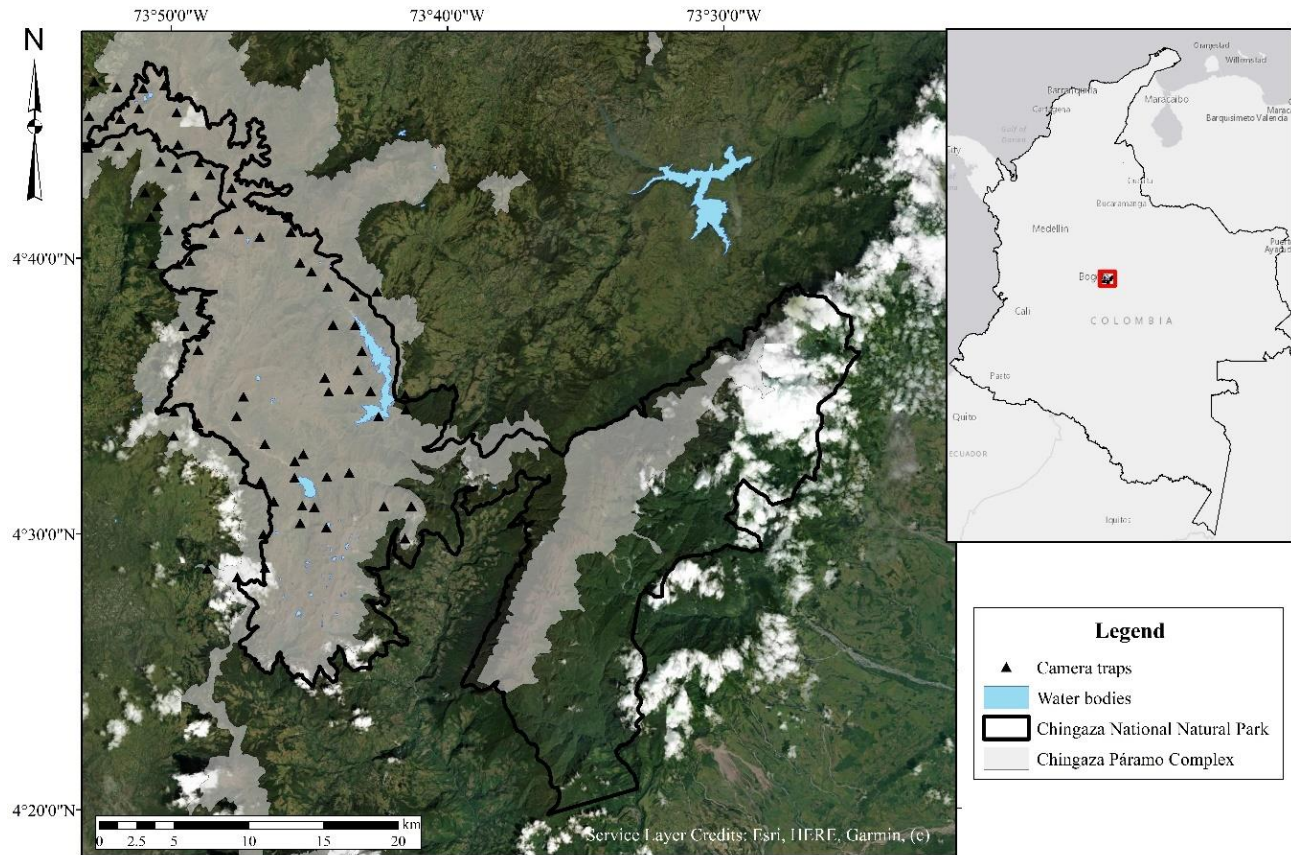


Figure 5. Location of the study area for assessing Andean bear (*Tremarctos ornatus*) occupancy in the context of Chingaza National Natural Park, Colombia.

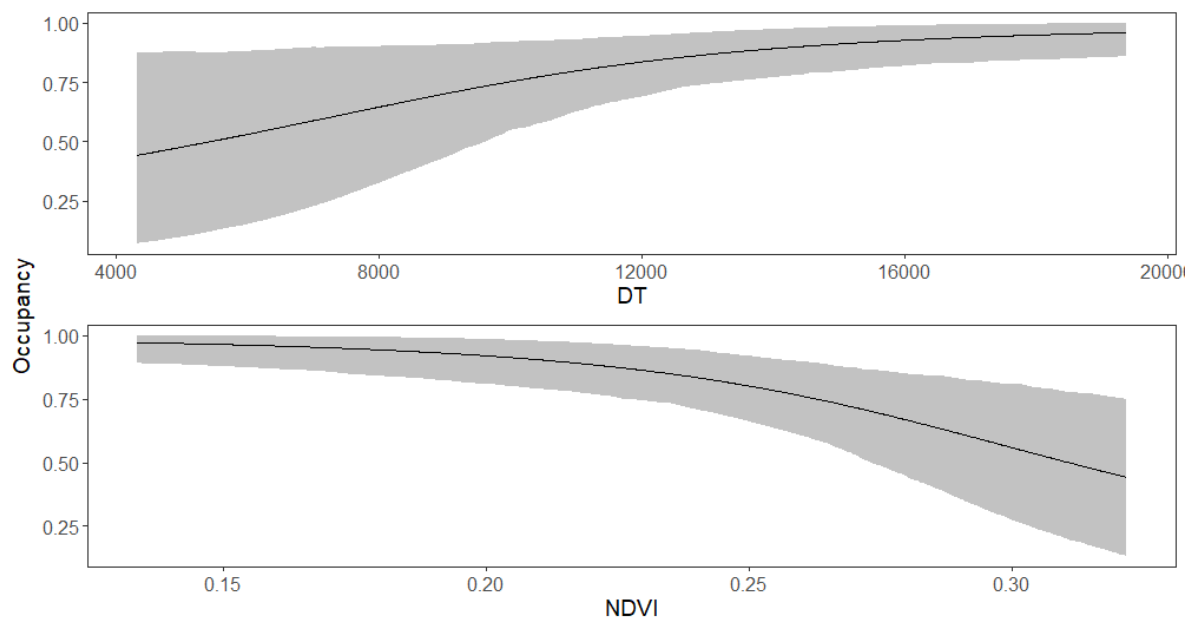


Figure 6. Response curves of Andean bear (*Tremarctos ornatus*) occupancy relative to covariate values. Bold lines represent posterior means and ribbons represent 95% Bayesian credible intervals. DT: Euclidean Distance to Towns (m). NDVI: Normalized Difference Vegetation Index range -1 to 1.

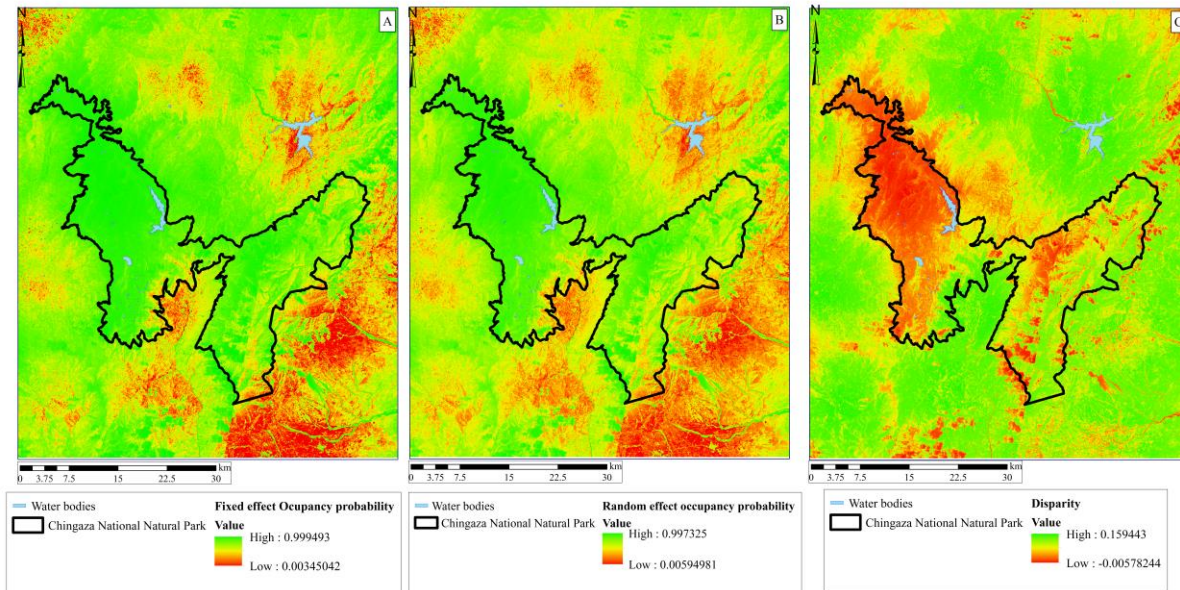


Figure 7. Predicted occupancy probability for Andean bear (*Tremarctos ornatus*) at the Chingaza Massif, Colombia. A. Fixed effect model, B. Random effect model, C. Disparity shows difference between predicted occupancy of Andean bear from fixed and random effects models, red areas are similar predictions and green areas shows greater disparity between predictions.

APPENDIX 3.

Novel insights into Andean bear home range in the Chingaza Massif Colombia

I. Mauricio Vela-Vargas, Juan Carlos Clavijo, Oscar Raigozo, Julian Zamora, Leonardo Arias-Bernal
and John L. Koprowski

(Published in International Bear News)

Novel insights into Andean bear home range in the Chingaza Massif, Colombia.

Ivan Mauricio Vela Vargas

Ph.D. (Cand) School of Natural Resources & the Environment. The University of Arizona.
Tucson, Arizona. USA.

Big Mammals Leader. The Wildlife Conservation Colombia. Bogotá, Colombia.

Associated Researcher. ProCAT Colombia. Bogotá. Colombia.

imvelavargas@email.arizona.edu

Juan Carlos Clavijo.

Director. Chingaza National Natural. Park. National Natural Parks of Colombia. La Calera,
Cundinamarca.

juan.clavijo@parquesnacionales.gov.co

Oscar Raigozo.

Ranger. Chingaza National Natural. Park. National Natural Parks of Colombia. La Calera,
Cundinamarca.

Julian Zamora.

Ranger. Chingaza National Natural. Park. National Natural Parks of Colombia. La Calera,
Cundinamarca.

Leonardo Arias Bernal

DVM M.Sc. Professor and Researcher. Uniagraria. Bogotá, Colombia.

Assistant profesor. El Bosque University. Bogotá. Colombia.

arias.leonardo@uniagraria.edu.co

John L. Koprowski.

Dean and professor. Haub School of Environment and Natural Resources. University of
Wyoming. Laramie. Wyoming. USA.

jkoprows@uwyo.edu

Studies about spatial ecology and telemetry of Andean bears (*Tremarctos ornatus*) are scarce due to limiting factors such funding, navigating adverse habitats, and the species' elusive behaviors (Castellanos, 2011; Garshelis, 2011). Knowledge about Andean bear home range have been extrapolated from studies performed in Ecuador and Bolivia (Paisley & Garshelis, 2006; Castellanos, 2011), but several authors caution against extrapolating information across systems not in equilibrium or those with heterogeneity (Elith & Leathwick, 2009). Andean bear home range sizes in other countries of occurrence are unknown. In Colombia, there have been exercises with VHF and GPS telemetry collars but home ranges have been not published and reports only focus on performance of devices (Rodríguez et al., 2016).

Intensive human development adjacent to protected areas influence the movement of individuals across large landscapes and may displace home range sizes (Castellanos 2011). Chingaza massif and its protected area has been a stronghold for Andean bear conservation in the east range of Colombia since 2010; monitoring programs in the country have identified more than 30 individuals (Parra-Romero et al., 2017). The protected area covers 78,294 ha with elevations that vary from 800 to 4,020 meters (Parques Nacionales Naturales de Colombia, 2016).

In 2018, an Iznachi trap (Castellanos, Jackson, & Arias L, 2016) was installed inside of the protected area and supervised for approximately 6 months. The trap was kept “open” to habituate individuals entering the trap baited with fruits, peanut butter, and different scents (Castellanos, Jackson, & Arias L, 2016). In June 2019, we captured one adult male (105 kg) and immobilized it using a mixture of Ketamine 4 mg/kg, Medetomidine 0.04 mg/kg and Midazolam 0.1 mg/kg with reversal agent Atipamezole 0.24 mg/kg (Arias-Bernal & Yarto-Jaramillo, 2019). We weighed, measured, and released the bear after it was fitted with a GPS collar (Telonics© TGW – 4577 GPS/Iridium). The collar operated from June 2019 to February 2020 when the activation of the dropoff system occurred and generated a total of 3,280 GPS fixes during that time.

We used the Minimum Convex Polygon (MCP) method to estimate the bear's home range at 189 km² for the 95% home range level and 67 km² for the 50% core area. We also used

Local Convex Hull (LoCoH) method, the 95% home range was 140 km² and the 50% core area was 13 km² (Figure 1, Figure 2). We used the `adehabitatHR` package (Calenge, 2006) to perform our calculations in R software (R Core Team, 2013)

We found LoCoH to be more reliable at capturing the heterogeneity of Chingaza protected area's landscape. MCP techniques can overestimate home ranges and include areas individuals avoid or are restricted from, whereas the LoCoH method identifies such spaces and captures physical boundaries of the landscape (Getz & Wilmers, 2004; Chirima & Owen-Smith, 2017).

Our home range estimates were smaller than for previous reports for Andean bear home ranges using 100% MCP and the total home range for nearest-neighbor convex hull (Castellanos, 2011). Castellanos (2011) found the 100% MCP home range of 3 males to be 125.8 km², whereas our results showed a large 95% MCP home range with a greater number of GPS fixes (412 locations for males). Using the LoCoH method, Castellanos (2011) reported total home range as 59.08 km² – less than half the area we found.

The 50% core areas was only 35.4% of the 95% home range suggesting the use of a relatively small areas with larger ranges representing opportunities for interindividual overlap, as suggested by Castellanos (2011). More individuals and telemetry data are needed to adequately test this hypothesis, and we encourage future researchers to examine Andean bear home range overlap in Colombia. Parra et al. (2019) reported different adult individuals scavenging a dead carcass in the Chingaza protected area without expressing antagonistic behaviors between them, lending some support of range overlap among individuals.

This was the first successful capture of an Andean bear in a protected area in Colombia. Here, we report the first known estimate of Andean bear home range in Colombia as well as the region. The results presented here serve to highlight the potential for future study with more individuals fitted with GPS collars. Future investigations of Andean bear spatial ecology can advance the knowledge of this charismatic species, inform best management actions, and serve to educate local communities that coexist with Andean bears.

Acknowledgements

We acknowledge the Chingaza protected area rangers for their invaluable help in the process. We are grateful to the Arizona Center for Nature Conservation/Phoenix Zoo, Reid Zoo Park, Wakata Biopark, and University of Arizona for their support, and the Fulbright – COLCIENCIAS Program in Colombia. Trapping and monitoring were performed under National Natural Parks of Colombia research permit #20182000007563.

Bibliography

- Arias-Bernal, L., and Yarto-Jaramillo, E. 2019. Medicine of captive Andean bears. Pages 548–554 in E. Miller, N. Lamberski, & P. Calle, Editors. Mill. - Fowler's Zoo Wild Anim. Med. Curr. Ther. Volume 9. Sounders.
- Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*. 197, 516–519.
- Castellanos, A. 2011. Andean bear home ranges in the Intag region, Ecuador. *Ursus* 22, 65–73.
- Castellanos, A., Jackson, D. A., & Arias L, L. 2016. Guidelines for the rescue, rehabilitation , release and post-release monitoring of Andean bears. Publisher. Quito.
- Chirima, G. J., and Owen-Smith, N. 2017. Comparison of kernel density and local convex hull methods for assessing distribution ranges of large mammalian herbivores. *Transactions in GIS* 21, 359–375.
- Elith, J., and Leathwick, J. R. 2009. Species distribution models: Empirical explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*. 40, 677–697.
- Garshelis, D. L. 2011. Andean bear density and abundance estimates — How reliable and useful are they? *Ursus* 22, 47–64.
- Getz, W. M., and Wilmers, C. C. 2004. A local nearest neighbor convex-hull construction of home ranges and utilization distribution. *Ecography*. 27, 1–17.
- Paisley, S., and Garshelis, D. L. 2006. Activity patterns and time budgets of Andean bears (*Tremarctos ornatus*) in the Apolobamba Range of Bolivia. *Journal of Zoology*. **268**, 25–34.
- Parques Nacionales Naturales de Colombia. 2016. Reformulacion participativa del plan de manejo Parque Nacional Natural Chingaza. Bogotá, Colombia. [In Spanish]

Parra-Romero, A., Galindo-T, R., Raigoso, E., Raigozo-hortua, O., Márquez, R., Bianchi, G., and Goldstein, I. 2017. Conservation status of the Andean bear *Tremarctos ornatus* at the Chingaza National Natural Park. Page 476 In M. Mills, X. Rueda Fajardo, & K. Shanker, editors. *28th Int. Congr. Conserv. Biol.* p. 476. Cartagena, Colombia: Society for Conservation Biology.

R Core Team. 2013. R: a language and environment for statistical computing. R Core team, Vienna, Austria. <<http://www.rproject.org>>.

Rodríguez, D., Reyes-Amaya, N., Reyes, A., Restrepo, H., Casas, Y., Salgado, O., Rodríguez, J., & Gómez, H. 2016. Desempeño de un collar GPS en el seguimiento a un oso andino (*Tremarctos ornatus*) en los Andes colombianos. *Revista Biodiversidad Neotropical*. 6, 68–76.

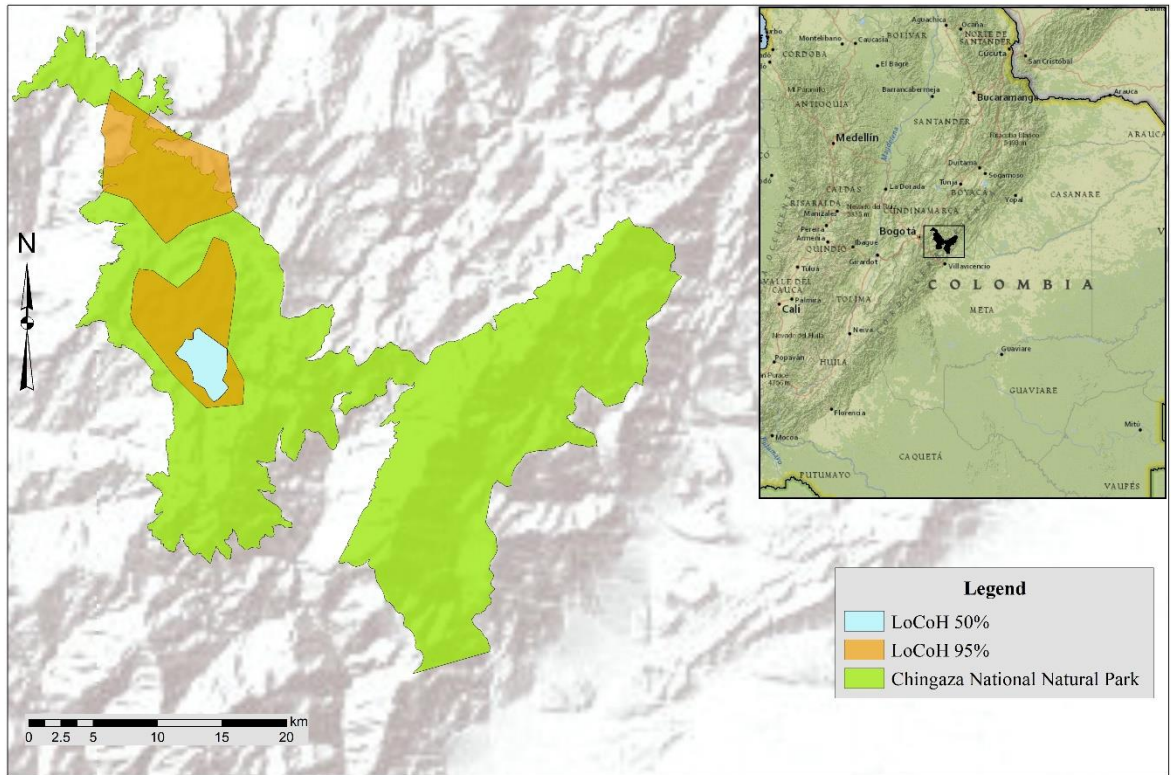


Figure 8. Home range of an individual of Andean bear (*Tremarctos ornatus*) captured at the Chingaza National Park, Colombia (Local Convex Hull method).

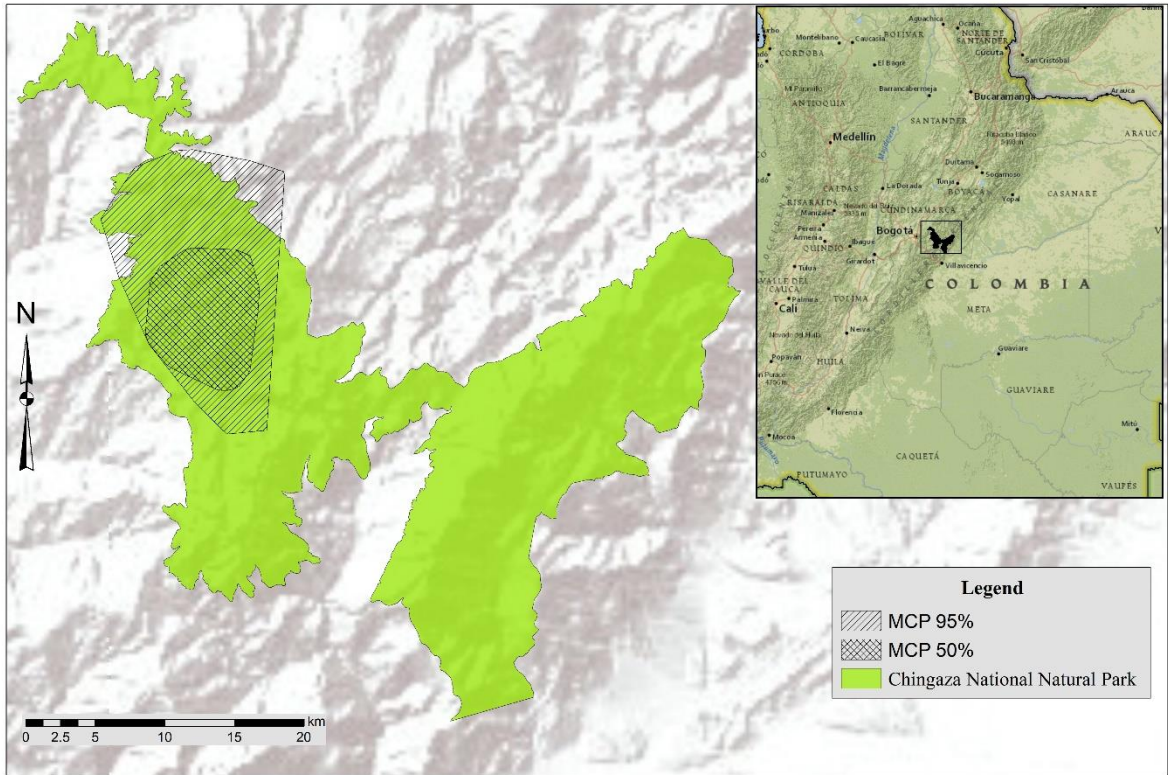


Figure 9. Home range of an individual of Andean bear (*Tremarctos ornatus*) captured at the Chingaza National Park, Colombia (MCP method).

APPENDIX 4.

Perception precedes reality? Interactions and opportunities for Andean bear conservation in the eastern range of Colombia

I. Mauricio Vela-Vargas, Jose R. Soto, Abu S.M.G Kibria, José F. González-Maya and John L. Koprowski

(Submitted to Biological Conservation)

Perception precedes reality? Interactions and opportunities for Andean bear conservation in the eastern range of Colombia

I. MAURICIO VELA-VARGAS ^{a,b,d}*

^a School of Natural Resources and the Environment, N335 environment and natural Resources 2, University of Arizona, Tucson, AZ, 85721, USA. imvelavargas@arizona.edu.

^b Wildlife Conservation Society – Colombia. Carrera 13 No. 77a-42, Bogotá, Colombia. (*Present address*). Telephone number: (+57) 314-437-5238

^d Proyecto de Conservación de Aguas y Tierras, ProCAT Colombia/International, Carrera 8 # 127c-36 Of. 101. Bogotá, Colombia

* Corresponding author

JOSE R. SOTO ^a

^a School of Natural Resources and the Environment, N335 environment and natural Resources 2, University of Arizona, Tucson, AZ, 85721, USA. jrs@arizona.edu

ABU S.M.G KIBRIA ^a

^a School of Natural Resources and the Environment, N335 environment and natural Resources 2, University of Arizona, Tucson, AZ, 85721, USA. akibria@arizona.edu

JOSE F. GONZALEZ-MAYA ^{c,d}

^c Departamento de Ciencias Ambientales, DCBS, Universidad Autónoma Metropolitana-Lerma, Av. De las Garzas 10, El Panteón, 520056 Lerma, Estado de México, Mexico.

jfgonzalezmaya@gmail.com

^d Proyecto de Conservación de Aguas y Tierras, ProCAT Colombia/International, Carrera 8 # 127c-36 Of. 101. Bogotá, Colombia

JOHN L. KOPROWSKI ^e

^e Haub School of Environment and Natural Resources, University of Wyoming, 201 Bim Kendall House, Laramie, WY 82072, USA. jkoprows@uwyo.edu

Highlights

- Magnitude of Human Andean Bear Conflicts is lower than perception of the conflicts in the Chingaza Massif, Colombia.
- Rural communities at Chingaza Massif prefer conservation programs rather than compensation of injured animals.
- Surveillance activities are priority in order to avoid Human Andean Bear Conflicts at the Chingaza Massif, Colombia.
- Including rural community's livestock concepts and practices could diminish human Andean bear negative interactions conflicts.

Abstract

Habitat loss due to human agriproduction practices are one of the main threats for Andean bear in South America. Establishment of livestock systems contributes to the generation of negative interactions between bears and human communities. These conflicts directly affect economic incomes of ranchers and generate negative perceptions towards the species, which can lead to retaliatory killings as has occurred in the past in Colombia. Objectives of our study were to characterize conflict triggers, assess perceptions, and evaluate the willingness to accept hypothetical conservation scenarios of Andean bears at the Chingaza Massif (Ch-M), east range of Colombia. Voluntary interviews were conducted with 145 adult ranchers in four

municipalities of the Ch-M. Positive response rate was 84% and the main reason for declining the interview was negative experience with past conservation projects. Main triggers of conflicts with Andean bears were surveillance monitoring activities. In proportion, 76% of those interviewed expressed a negative perception towards Andean bears influenced by past conflicts, duration of ownership of the farm and perceived abundance of bears. Ranchers preferred development of conservation projects that do not include payment for loss of cattle, showing a higher willingness to accept conservation projects that include their local knowledge in livestock practices. Evaluation of perceptions of rural communities regarding the presence of wildlife, particularly large carnivores such as Andean bears, is an essential input when generating mitigation and prevention tools for conflict events.

Keywords

Tremarctos ornatus, negative interactions, Human-wildlife conflicts, protected areas, interviews, co-existence.

1. Introduction

Conflicts that involve human communities and wildlife, particularly carnivores, is an increasing concern for conservationists and wildlife managers (Messmer, 2009; van Eeden et al., 2018b). Such conflicts are the result or defined by a varied set of interactions that involve ecological and socio-economic factors, including continuous increase of human population, the overlap between humans and wildlife habitats, economic and non-economic losses and, even livelihoods of human communities around the world (Marchini, 2014; Redpath et al., 2015; Borah et al., 2018; Cusack et al., 2021; Fall & Jackson, 2002; Ripple et al., 2014). Human – Wildlife conflicts (HWC) concept was recently described as: controversies that emerged because the presence or

behavior of wildlife represents real or perceived threat to human interests, leading to discussions and disagreements between groups of humans (in favor or against wildlife) and negative impacts on people and/or wildlife (IUCN, 2020; Zimmermann et al., 2020). Thus, HWC conflicts occur across the world and under multiple conditions, contexts, and underlying processes, with multiple degrees of severity depending on the very nature of the interaction.

Andean bears (*Tremarctos ornatus*) and human communities have long cohabited the tropical Andean region in South America. As human density increases and space use by local communities expand, overall human and Andean bear interactions increase, and when interactions are negative at any level, Human – Andean Bear Conflicts (HABC) arise and have also increased over time (Jorgenson, Sandoval, 2005, Goldstein et al., 2006 Andrade et al., 2019). The increase in the frequency and severity of HABC is considered as a main threat to the species survival (Goldstein et al., 2006, Ministerio Del Medio Ambiente, 2001, Vela-Vargas et al., 2021, Velez–Liendo, Garcia-Rangel, 2017).

Human economies are affected by HABC through the loss of livestock or crops, and people are prone to invest in poor conflict management strategies misguided by anecdotal knowledge (Goldstein et al., 2006; Sánchez-Mercado et al., 2008; Marchini, 2014). These dynamics are the consequence of human activities such as livestock and agriculture in high elevation paramo grasslands and cloud forests that produce changes on soil use and habitat availability for Andean bears (Kattan et al., 2004; Armenteras et al., 2003), resulting in increased HABC that often lead to retaliatory bear killings (Figueroa, 2015; Gárrido Corredor et al., 2021). Colombian authorities have recorded at least 8 bears killed by human communities in retaliation between 2016-2020, likely an underestimation of actual bear killings. These dynamics generate a one-way scenario

where successful resolution or mitigation of HABC is now a mandatory aspect of Andean bear conservation efforts in Colombia (Rodríguez-Páez et al., 2016; González-Maya et al., 2017).

The Chingaza Massif is located on the east Andean range of Colombia and is one of the regions where HABC have been studied more extensively. Negative interactions are reported constantly, and retaliatory killings have been recorded with legal consequences for people involved (Parra-Romero et al., 2019; Gárrido Corredor et al., 2021; Parra-Romero et al., 2017).

Mitigation and conflict management plans require information such as magnitude of the HABC, perceptions of rural communities towards wildlife and potential solutions including the needs of rural communities (Haab & McConnell, 2002; Marchini et al., 2021; van Eeden et al., 2018a).

Previous research about human communities' perception towards Andean bear conservation actions in the Chingaza Massif showed that rural communities have been marginalized, but triggers, and potential solutions for HABC have not been identified in the region (Jorgenson and Sandoval, 2005; Parra-Romero, 2011; Parra-Romero et al., 2019b).

Our study aims to evaluate magnitude of HABC including the triggers of these interactions and assess hypothetical conservation scenarios for Andean bear on the Chingaza Massif, Colombia.

We hypothesized that the magnitude of the conflicts will be better explained by livestock practices. Also, we assessed the perceptions of human communities towards Andean bears on the Chingaza Massif and compared with the magnitude of the conflict events. We hypothesized that negative perception towards the species will be higher than magnitude of HABC in the region. In addition, we evaluated how landowners' values influence attitudes towards Andean bears and their receptivity to implementing strategies to reduce conflict in the region. We hypothesized that

ranchers would prefer programs that compensate for cattle loss due to the HABC over other types of management actions.

TABLE 1.

2. Material and methods

2.1 Study Area

The Chingaza Massif is located between Boyacá, Cundinamarca, and Meta departments on the east range of Colombia with an elevation varying from 500 to 4100 m and includes The Chingaza National Natural Park (Ch-NNP), a 766 km² protected area that extends to prohibit wildlife killing and control cattle grazing (Figure 1) Precipitation regime is monomodal ranging between 2000 – 3600 mm/year, with a rain peak between May and August followed by lower precipitation rates between December and February (Morales Rivas et al., 2007; Vargas Rios & Pedraza, 2004). Main habitats present in the massif include Andean forest and paramo ecosystems distributed between Cundinamarca and Meta departments (Parques Nacionales Naturales de Colombia, 2016). The Chingaza Massif provides the majority of water for Bogotá, the largest (>7,180,000 people), and capital city of Colombia and 11 municipalities in the region (Vargas Rios & Pedraza, 2004). Main agriproduction activities in the massif include traditional high elevation ranching, agriculture and subsistence farming (Garavito González et al., 2018; Pedraza et al., 2020).

FIGURE 1.

2.2 Data collection

Data were collected from 2017 to 2019 in areas adjacent to Ch-NNP in localities with previous HABC conflict reports. We employed semi-structured questionnaires to record the magnitude of

HABC and perceptions towards the species in the massif (Dillman et al., 2014; White et al., 2005). Questionnaires were made to people 18 years old or older (legal adulthood in Colombia). Participation was voluntary and no incentives were provided for responding to the questionnaire. The questionnaire consisted of questions organized in five subjects: 1. Demographics, 2. Wildlife uses, 3. Economic activities and productive systems, 4. Conflict event characteristics and, 5. Perception of the species. (González-Maya et al., 2013; Márquez & Goldstein, 2014). Questionnaire parameters were approved by the Institutional Review Board of the University of Arizona (IRB approval 1705451796). Informed consent was obtained before participants answered any question (all the documents were translated and supplied in Spanish). The questionnaires were administered in person, in the context of a formal interview on each farm in a private place where the interviewee felt comfortable to respond (Dillman et al., 2014). To evaluate landowners' willingness to accept (WTA) compensation for conflict mitigation at the Chingaza Massif, we used attributes from other studies and applied to the social and economic context of the Chingaza Massif (Neupane et al., 2017; Manoa et al., 2021). Our questionnaire included questions on five program attributes: type of payment, farm area, time of hypothetical project, implementer, and monetary compensation (Table 1.). Selected attributes and levels were evaluated from available ecosystem services payment programs implemented in Colombia (BanCO2), and the cost for lost cattle was obtained from local markets at the massif. In order to analyze WTA scenarios, we presented hypothetical scenarios in the most efficient manner (e.g. improved orthogonality and shortest survey length) following the recommendations provided by (Soto et al., 2016), and we generated 8 hypothetical scenarios of discrete choice: 1 accepted, and 0 otherwise.

2.3 Data analysis

2.3.1 Conflict triggers at Chingaza Massif

We used descriptive statistics to analyze the socioeconomic profile of the villagers at the Chingaza Massif. Generalized linear models (GLM) were performed to evaluate how demographics, economic activities, and productive systems management affected the fact of recording HABC and identify the main triggers of negative interactions. We defined 9 variables and used a stepwise procedure to generate a list of 32 models. The Akaike Information Criterion (AIC) was calculated for each model, afterwards we ranked and selected the best models using ΔAIC values (Anderson et al., 1994). We calculated model-averaged coefficients for covariates with $\Delta AIC < 2$.

2.3.2 Perceptions towards Andean bears at Chingaza Massif

In the same way, GLMs were used to evaluate how demographics, economic activities and HABC affected the local perception towards Andean bears. We defined 12 variables and used the same process mentioned above. We only applied additive combinations among variables to keep the set of variables to a reasonable size and identify variables that triggered HABC and generated positive/negative perceptions towards the species. Correlation analyses were performed to identify and eliminate highly correlated variables and reduce multicollinearity among independent variables (Zuur et al., 2009).

2.3.3 Willingness to accept hypothetical scenarios at Chingaza Massif.

For WTA data, we performed random effects models (REMs) to adjust unobserved heterogeneity at the individual level. REMs allow covariance among the hypothetical scenarios (Horowitz &

McConnell, 2002). Analyses were performed in R (R TEAM DEVELOPMENT CORE, 2008) using the packages lme4 and plm (Bates et al., 2015; Croissant & Millo, 2008).

3. Results

We interviewed 145 people with a positive response rate of 84%. The main reason for choosing to not participate was lack of trust in the researcher and the project (n=15, 65%) due to past experiences with other Andean bear conservation projects in the region. All respondents who did not respond to the interview were males between 35-50 years old. Of the 122 respondents that accepted participation in the questionnaire, 60% of the respondents were males, 40% females. 88% of the respondents presented an average age of 53 (± 15) years old. Census data showed that in our study area the proportion of women and men is 50:50 (DANE 2018). Most respondents (71%) expressed that they only had primary school studies and 27% reported basic secondary school studies. The main source of economic income was livestock (sheep and cattle) activities (92%).

3.1 Human – Andean bear conflicts dynamics

For HABC evaluation, we found that conflict events were explained if ranchers guarded cattle, reporting more conflict events when they did not often supervise cattle with no conflicts when cattle were supervised (Table 2). On average ranchers left cattle unsupervised 10 (± 9) days in the highlands. We used the number of days that ranchers usually leave cattle without supervision, but due to the lack of responses to this question, this variable was not selected for our analysis. In addition, younger people are more likely to note conflicts than older people. Economic losses from the last two years derived from Andean bear attacks were on average USD\$1047 (\pm \$621) for cattle and USD\$1822 (\pm \$1849) for sheep.

TABLE 2.

3.2 Perceptions towards Andean bears

People expressed negative perceptions of Andean bears in Chingaza Massif; 76% of interviewees shared negative comments. The negative perception of Andean bears is influenced by past events of negative interaction with the species, and because people generally believe that bears only live inside of the protected area and is not common to report individuals outside of Ch NNP (Table 3). Perceived abundance of the species is related to the time that people that have lived on the massif; people that lived for more time in the study area perceive Andean bear as common and, tend to express positive perceptions towards bears.

TABLE 3

Interviewees reported that HABC have decreased during the last 5 years (62%) whereas 38% of the people believe that the problem increased or has remained stable; 69% of the interviewees expressed concern about having Andean bears near their farms.

When evaluating perceptions of the Andean bear (positive or negative), we found that rural ranchers expressed negative perceptions of the species when presented past conflicts with the species, and people that perceived Andean bears as rare in the area are less likely to present positive perceptions than people that perceive the species as common, an unexpected result.

Ranchers who have been owners for less time in the area are more likely to express negative perceptions towards bears, whereas people with longer ownership history tend to show positive perceptions.

We found that women perceived Andean bears as a rare or very rare species, adding that women perceive environmental laws as tools to educate rural communities, conversely, men perceived bears as a common species at the Chingaza Massif. People that expressed positive attitudes

towards Andean bears believe that laws are positive, and they regulate human activities, whereas people that expressed negative perceptions to bears do not agree in general with laws because these punish people (Figure 2).

FIGURE 2

3.3 Willingness to accept conservation scenarios.

Of the 122 responses, 79 respondents were complete and permitted WTA analyses (Table 4). Contrary to our hypothesis, ranchers at Chingaza Massif tend to prefer hypothetical scenarios where projects pay for the maintenance of natural areas over the payment for loss of cattle due to HABC ($p= 0.07$), in programs that include more than 5% of their farms ($p=0.07$). The shortest duration of a project presented a negative significant relationship ($p<0.05$), which means that people reject short time Andean bear conservation projects (in our hypothetical scenario < 2 years).

TABLE 4

As expected, ranchers tend to choose the highest amount allowed in our hypothetical scenario as compensation (\$87 USD/ha; $p<0.001$). An important result showed a negative relationship of the type of agency executing the projects ($p<0.01$) in this case NGO's, rural ranchers preferred that government environmental agencies directly execute the projects over other institutions.

4. Discussion

Finding ways to mitigate conflicts and promote coexistence of humans and carnivores is a key challenge for conservation, especially for Andean bears (Jorgenson & Sandoval, 2005b).

Deforestation and human population increase in areas near to protected areas further exacerbate HABC (Kattan et al., 2004) as well as the negative perceptions. Negative interactions have been

reported during the last 10 y at the Chingaza Massif (Parra-Romero et al., 2019a, 2017), but the magnitude of HABC are lower than the perception of the interactions, our results showed that only a small proportion of ranchers (28%) reported HABC, but the general idea of communities along the Chingaza Massif towards the Andean bears is that bears are “bad for the business,” supporting similar reports in the central range of Colombia (Escobar-Lasso et al., 2020).

We identified that 28% of the ranchers reported past HABC, whereas negative perceptions were expressed by greater than 70% of respondents in the Chingaza Massif, meaning that people believe that Andean bears affect livestock systems more than the actual problems that have been reported. HABC are real on the Chingaza Massif but are not as frequent nor as profound as people believe. These results are similar to other studies in countries such as Perú and Ecuador (Andrade et al., 2019; Figueroa, 2015) where perceptions are negative because of oral traditions and despite a lack of evidence for the negative events (Goldstein et al., 2006).

The main trigger of HABC at the Chingaza Massif is the lack of surveillance of domestic animals that are managed in remote areas for grazing, this is a traditional practice applied in the Andean region of Colombia and more broadly across South America (Jorgenson & Sandoval, 2005a; Goldstein, 2002; Goldstein et al., 2006a). Implementation of surveillance livestock programs reduced attacks on cattle by 42 – 100% for other carnivore species (Miller et al., 2016; van Eeden et al., 2018b), but these stewardship strategies need to be tested at the Chingaza Massif and other regions of Colombia.

Rural ranchers expressed that they do not receive technical support from government agencies to improve management and protection of livestock systems. In general, most ranchers maintain minimal cattle management conditions, because its low cost and practices that have been passed

on across generations in the highlands of Colombia and South America (Goldstein et al., 2006).

Additionally, funding possibilities are scarce to improve livestock management and environmental agencies tend to perform reactive and not proactive responses to HABC.

Husbandry changes were made by ranchers only after experiencing damage by Andean bears, showing a reactive response to the problem, and not an initiative-taking approach towards prevention. This kind of management is traditional in Colombia and other regions of the neotropics that experienced conflict with large carnivores (Amit & Jacobson, 2017).

Change of livestock practices such as implementing electric fencing could be an effective management tool for reducing HABC (Zukowski and Ormsby, 2016), but not the only one, the dynamics of the HABC are complex and implementation of surveillance programs with the improvement of the productive activities could help to design mitigation and management programs of HABC, all these actions should be complemented with environmental workshops to facilitate adoption by human communities.

Perceptions towards HABC can be exacerbated by different causes such as the lack of attention by public environmental agencies to HABC reports and the cost associated with recording and monitoring of conflict events (Jorgenson and Sandoval, 2005). Additionally, environmental agencies in Colombia present high turnover of personnel and gaps in their monitoring programs (Hohbein et al., 2021). These practices can generate mistrust by ranchers of environmental agencies, as have been reported in other regions of Colombia and South America (Cusack et al., 2021; Escobar-Lasso et al., 2020; Young et al., 2010; Zukowski and Ormsby, 2016).

One way to mitigate and generate positive perception towards Andean bears is the implementation of conservation compliance programs that generate conservation incentives and

at the same time improve of the productivity of ranching systems, these kinds of programs have been effective in diminishing deforestation rates in the neotropics (Ogg, 2020). Generation of voluntary conservation agreements between ranchers and environmental agencies have had positive outcomes in other areas of Colombia (Koprowski et al., 2019; Orjuela et al., 2020), demonstrating improvement of the well-being of human communities, appropriation of conservation programs and decrease of conflict events with large carnivores. The *Conservamos la Vida* (We preserve life) initiative, has been working with ranchers and coffee producers in the western and central ranges of Colombia to implement conservation agreements to improve production practices (livestock and agriculture) as well as conservation areas inside of private properties for Andean bears (Acevedo et al., 2019). These conservation programs linked with environmental education schemes in rural communities led to changed negative perceptions towards the Andean bears (Espinosa and Jacobson, 2012).

Programs such the mentioned bellow could be part of the management for HABC at the Chingaza Massif. Ranchers see an opportunity for conservation of paramos and cloud forest, because these communities understand the importance of the ecosystem services provided by these ecosystems and envision the Andean bear as an opportunity for ecotourism (Pedraza et al., 2020). The main obstacle for the implementation of conservation programs is that rural communities perceive that authorities should be more proactive and less reactive in the management of HABC, an identified problem in the past that has not yet been resolved (Garavito González et al., 2018).

Identification of the HABC triggers and perceptions towards the species is a first step in order to find coexistence tools between ranchers and bears (Marchini et al., 2021). Livestock depredation

is the main interaction reported with Andean bears at the Chingaza Massif, a pattern seen throughout Andean South America (Figueroa, 2015; Zukowski and Ormsby, 2016) and mitigation tools have been not applied systematically to manage these interactions. By using WTA compensation hypothetical scenarios, our results are consistent with general results from other studies about revenue, where ranchers prefer higher income (Amit and Jacobson, 2017; van Eeden et al., 2018), but contrary to our hypothesis, ranchers preferred projects that involved large scale conservation of their lands over the payment for lost cattle, it is important to state that compensation programs for loss of cattle or replacement of attacked animals in Colombia never have been implemented and are not approved by environmental authorities. This presents a perfect opportunity to generate programs that involve rural communities in their own conservation programs, on their lands and with their knowledge where the main conditions are not imposed by an external agent but applied with a mix of local traditional ecological knowledge and practices on livestock systems leading to a real and perceived control of cattle and the adoption of sustainable productive practices (Bruskotter and Wilson, 2014).

5. Conclusions

The evaluation of conflicts, both past and present, perceptions of communities and the willingness to find a solution to the conflicts by affected people, must be a priority that involves rural communities in conservation programs, maintaining systematic and replicable approaches (Zimmermann et al., 2020). Examples of these exercises have been applied for brown bear (*Ursus arctos*) conservation in Europe with positive results in order build conservation and conflict mitigation scenarios seeking mutual adaptation and conviviality between rural communities and brown bears (Toncheva and Fletcher, 2021). Tools such as relocation have

been applied for Black bears in Great Smoky Mountains National Park (USA), with success in minimizing black bear – human conflicts (White et al., 2022), but in comparison with Colombia, there are not tools or plans for monitoring problematic individuals, and relocation of Andean bears individuals across the country is not suggested given the limitation in evaluating health status of populations and potential movements of pathogens among bear populations. Is because this, considering beliefs and perspectives from local communities complementing conservation programs with environmental education will enable ranchers and farmers to be leaders in protecting highland ecosystems paramos and Andean bears.

Recent studies demonstrated that negative interactions and perceptions between human communities and wildlife in general are related to economic losses (e.g. cattle or crops), but new findings showed intangible drivers that are also related such as social, cognitive and emotional factors that lead to the negative reactions towards wildlife, especially carnivores (Álvarez and Zapata-Ríos, 2021; Ballejo et al., 2022; Marchini et al., 2021). Our study showed how cultural, economic and management drivers affect the complex dynamics of Human – Andean Bear Conflicts, and the uniqueness of each locality where conflicts are reported. Herein, we were able to merge different approximations in a systematic way that can be applied in any context and geographical region for the identification of triggers and management tools for Andean bears across their range.

CRedit authorship contribution statement

I. Mauricio Vela-Vargas: Conceptualization, Investigation, Writing - Original draft, Formal analysis, Methodology, Funding acquisition, Project administration. **Jose Soto:** Methodology, Data Curation, Writing – Review & Editing. **Abu S.M.G. Kibria:** Methodology, Formal

Analysis, Writing – Review & editing. **José F. González-Maya**: Methodology, Formal analysis, Writing – Review & editing, Visualization. **John L. Koprowski**: Conceptualization, Resources, Writing – Original Draft, Writing – Review & editing, Visualization, Funding acquisition, Supervision.

Acknowledgments

Thanks to the rangers of Chingaza National Natural Protected Area, especially to Oscar Raigozo and Julian Zamora for their companionship and help in the interview process. To Juan Camilo Rubiano, Camilo Paredes and Fernando Alvarez for their effort in the field, long walks and company in the data collection process. To the communities of San Juanito and El Calvario (Meta), Choachí, La Calera and Guasca (Cundinamarca) for their willing to participate in this research. This research was funded by IMV-V COLCIENCIAS-Fulbright scholarship, College of Agriculture and Life Science of the University of Arizona, The Conservation grant award of Arizona Center for Nature Conservation – Phoenix Zoo and Reid Zoo Park.

Bibliography

- Acevedo, C., Celis, J., Cuevas, D., Giraldo, M., Lievano, I., Marquez, R., Maya, A.M., Parra, N., Rincon, L., Roncancio, N., Salazar, M., Silva, F., Troncoso, J.C., Villegas, M.C., 2019. Conservamos la Vida : Patrones de ocupación y diagnóstico de paisaje de conflicto entre el oso andino y la gente en la Unidad Núcleo de Conservación Tatamá - Farallones - Munchique. Andean Bear Conservation Aliance, Cali.
- Álvarez, H.G., Zapata-Ríos, G., 2021. Do social factors influence perceptions of the jaguar *Panthera onca* in Ecuador? *Oryx* 56, 1–8. <https://doi.org/10.1017/s003060532000054x>
- Amit, R., Jacobson, S.K., 2017. Stakeholder barriers and benefits associated with improving livestock husbandry to prevent Jaguar and Puma depredation. *Human Dimensions of Wildlife* 1209, 1–21. <https://doi.org/10.1080/10871209.2017.1303099>
- Anderson, D.R., Burnham, K.P., White, G.C., 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75, 1780–1793. <https://doi.org/10.2307/1939637>

- Andrade, M., Espinoza, G., Moncada, J., 2019a. Percepción de actores clave acerca del conflicto ser humano-oso en la parroquia Plaza Guitiérrez, Íntag, Imbabura, Ecuador. *Mammalia aequatorialis* 1, 43–50.
- Andrade, M., Espinoza, G., Moncada, J., 2019b. Percepción de actores clave acerca del conflicto ser humano-oso en la parroquia Plaza Guitiérrez, Íntag, Imbabura, Ecuador. *Mammalia aequatorialis* 1, 43–50.
- Armenteras, D., Gast, F., Villareal, H., 2003. Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes , Colombia. *Biol Conserv* 113, 245–256. [https://doi.org/10.1016/S0006-3207\(02\)00359-2](https://doi.org/10.1016/S0006-3207(02)00359-2)
- Ballejo, F., Plaza, P., di Virgilio, A., Lucherini, M., Gáspero, P., Guerisoli, M., Novaro, A., Funes, M., Lambertucci, S., 2022. Unravelling negative interactions between humans, mammalian carnivores and raptors in South America. *Ecologia Austral* 32.
- Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Borah, J., Jyoti Bora, P., Sharma, A., Dey, S., Sarmah, A., Vasu, N.K., Sidhu, N., 2018. Livestock depredation by Bengal tigers in fringe areas of Kaziranga Tiger Reserve, Assam, India: implications for large carnivore conservation. *Human-Wildlife Interactions* 12, 186–197.
- Bruskotter, J.T., Wilson, R.S., 2014. Determining where the wild things will be: Using psychological theory to find tolerance for large carnivores. *Conserv Lett* 7, 158–165. <https://doi.org/10.1111/conl.12072>
- Croissant, Y., Millo, G., 2008. Panel data econometrics in R: The plm package. *J Stat Softw* 27, 1–43. <https://doi.org/10.18637/jss.v027.i02>
- Cusack, J.J., Bradfer-Lawrence, T., Baynham-Herd, Z., Castelló y Tickell, S., Duporge, I., Hegre, H., Moreno Zárate, L., Naude, V., Nijhawan, S., Wilson, J., Zambrano Cortes, D.G., Bunnefeld, N., 2021. Measuring the intensity of conflicts in conservation. *Conserv Lett* 14:e12783, 1–11. <https://doi.org/10.1111/conl.12783>
- Dillman, D., Smyth, J., Christian, L.M., 2014. Internet, Phone, Mail, and Mixed-mode surveys. The tailored design method, Fourth edi. ed. Wiley, New Jersey.
- Escobar-Lasso, S., Cepeda-Duque, J., Gil-Fernandez, M., González-Maya, J.F., 2020. Is the banana ripe? - Andean bear-human conflict in a protected area of Colombia. *Human - Wildlife Interactions* 14, 1–17.
- Espinosa, S., Jacobson, S.K., 2012. Human-Wildlife conflict and environmental education: Evaluating a community program to protect the Andean bear in Ecuador. *J Environ Educ* 43, 55–65. <https://doi.org/10.1080/00958964.2011.579642>
- Fall, M.W., Jackson, W.B., 2002. The tools and techniques of wildlife damage management - Changing needs: An introduction. *Int Biodeterior Biodegradation* 49, 87–91. [https://doi.org/10.1016/S0964-8305\(01\)00107-X](https://doi.org/10.1016/S0964-8305(01)00107-X)
- Figuroa, J., 2015. Interacciones humano–oso andino *Tremarctos ornatus* en el Perú: consumo de cultivos y depredación de ganado. *Therya* 6, 251–278. <https://doi.org/10.12933/therya-15-251>
- Garavito González, L., Gómez Zárate, D.P., Palacio Tamayo, D., 2018. Gobernanza territorial en los páramos Chingaza y Sumapaz-Cruz Verde. Una comparación de sus principales actores y problemáticas. *Perspectiva Geográfica* 23, 11–30. <https://doi.org/10.19053/01233769.6703>
- Gárrido Corredor, A.M., Cottyn, H., Martínez-Medina, S., Wheatley, C., Sáncnez, A., Kirshner, J., Cowie, H., Touza-Montero, J., White, P.C.L., 2021a. Oso , osito ¿ A qué venís? Andean bear

- conflict , conservation , and campesinos in the Colombian Páramos. *Sustainability* 13, 1–18. <https://doi.org/https://doi.org/10.3390/su131910489>
- Goldstein, I.R., 2002. Andean bear-cattle interactions and tree nest use in Bolivia and Venezuela. *Ursus* 13, 369–372.
- Goldstein, I. R., Paisley, S., Wallace, R., Jorgenson, J.P., Cuesta, F., Castellanos, A., 2006a. Andean bear – livestock conflicts: a review. *Ursus* 17, 8–15. [https://doi.org/10.2192/1537-6176\(2006\)17](https://doi.org/10.2192/1537-6176(2006)17)
- González-Maya, J.F., Galindo-Tarazona, R., Urquijo-Collazos, M.M., Zárate-Vanegas, M., Parra-Romero, A., 2017. *El Oso Andino en el Macizo de Chingaza*. Bogotá, Colombia.
- González-Maya, J.F., Vela-Vargas, I.M., Zárate-Charry, D.A., Pineda-Guerrero, A., Cepeda, A.A., Arias-Alzate, A., Balaguera-Reina, S.A., 2013. Definición metodológica del Plan de Conservación de Felinos del Caribe colombiano: lineamientos generales, in: *Plan de Conservación de Felinos Del Caribe Colombiano: Los Felinos y Su Papel En La Planificación Regional Integral Basada En Especies Clave*. pp. 35–48.
- Haab, T., McConnell, K., 2002. *Valuing environmental and Natural resources: The econometrics of non-Market valuation*. Edward Elwar Publishing, Northampton.
- Hohbein, R.R., Nibbelink, N., Cooper, R.J., 2021. Impacts of decentralized environmental governance on Andean bear conservation in Colombia. *Environ Manage* 68, 882–899. <https://doi.org/10.1007/s00267-021-01532-4>
- Horowitz, J.K., Mcconnell, K.E., 2002. A Review of WTA / WTP Studies. *J Environ Econ Manage* 44, 426–447.
- IUCN, 2020. IUCN SSC Position Statement on the Management of Human-Wildlife Conflict. IUCN Species Survival commission (SSc) Human-Wildlife conflict Task Force.
- Jorgenson, J., Sandoval, S., 2005. Andean bear management needs and interactions with humans in Colombia. *Ursus* 16, 108–116. [https://doi.org/10.2192/1537-6176\(2005\)016\[0108:ABMNAI\]2.0.CO;2](https://doi.org/10.2192/1537-6176(2005)016[0108:ABMNAI]2.0.CO;2)
- Kattan, G., Hernández, O.L., Goldstein, I., Rojas, V., Murillo, O., Gómez, C., Restrepo, H., Cuesta, F., 2004. Range fragmentation in the spectacled bear *Tremarctos ornatus* in the northern Andes. *Oryx* 38, 155–163. <https://doi.org/10.1017/S0030605304000298>
- Koprowski, J.L., González-Maya, J.F., Zárate-Charry, D.A., Sharma, U., Spencer, C., 2019. *Local Approaches and Community-Based Conservation*, in: Koprowski, J.L., Krausman, P.R. (Eds.), *International Wildlife Management Conservation Challenges in a Changing World*. Johns Hopkins University Press, Baltimore.
- Manoa, D.O., Mwaura, F., Thenya, T., Mukhovi, S., 2021. Comparative analysis of time and monetary opportunity costs of human-wildlife conflict in Amboseli and Mt . Kenya Ecosystems , Kenya. *Current Research in Environmental Sustainability* 3, 1:12. <https://doi.org/https://doi.org/10.1016/j.crsust.2021.100103>.
- Marchini, S., 2014A. Who’s in Conflict with Whom? Human Dimensions of the Conflicts Involving Wildlife, in: Penteado, M., Silva, W.R., Verdade, L.M. (Eds.), *Applied Ecology and Human Dimensions in Biological Conservation*. Springer, Berlin, pp. 189–209. <https://doi.org/10.1007/978-3-642-54751-5>
- Marchini, S., Ferraz, K.M.P.M.B., Foster, V., Reginato, T., Kotz, A., Barros, Y., Zimmermann, A., Macdonald, D.W., 2021. Planning for human-wildlife coexistence: conceptual framework, workshop process and a model for transdisciplinary collaboration. *Frontiers in Conservation Science* 2:752953, 1–11. <https://doi.org/10.3389/fcosc.2021.752953>

- Márquez, R., Goldstein, I., 2014. Manual para el reconocimiento y evaluación de eventos de depredación de ganado por carnívoros silvestres, Version 1. ed. Wildlife Conservation Society Colombia, Santiago de Cali. <https://doi.org/10.13140/2.1.4604.0643>
- Messmer, T., 2009. Human – wildlife conflicts : emerging challenges and opportunities. *Human-Wildlife Conflicts* 3, 10–17.
- Miller, J.R., Stoner, K.J., Mikael, Cejtin., Meyer, T., Middleton, A., Scmitz, O., 2016. Effectiveness of Contemporary Techniques for Reducing Livestock Depredations by Large Carnivores. *Wildl Soc Bull* 40, 806–815. <https://doi.org/10.1002/wsb.720>
- Ministerio Del Medio Ambiente, 2001. Programa nacional para la conservación en Colombia del Oso Andino *Tremarctos ornatus*. Bogotá, Colombia.
- Morales Rivas, M., Otero García, J., van der Hammen, T., Perdigón, A., Cadena Vargas, C., Pedraza Peñaloza, C., Rodríguez Eraso, N., Franco Aguilera, C., Betancourth Suárez, J., Olaya Ospina, E., Posada Gillede, E., Cárdenas Valencia, L., 2007. Atlas de páramos de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia.
- Neupane, D., Kunwar, S., Bohara, A.K., Risch, T.S., Johnson, R.L., 2017. Willingness to pay for mitigating human-elephant conflict by residents of Nepal. *J Nat Conserv* 36, 65–76. <https://doi.org/10.1016/j.jnc.2017.02.004>
- Ogg, C., 2020. Transforming farm-program incentives to preserve tropical forests. *Conservation Biology* 34, 762–765. <https://doi.org/10.1111/cobi.13393>
- Orjuela, S., Valenzuela, L., Saavedra, C.A., Herrera, A., Aguirre, E., Castro, P., Parada, M., Orrego, O., 2020. Acuerdos de conservación. Un pacto con la sociedad civil, un camino hacia la sostenibilidad ambiental. Proyecto Vida Silvestre, Bogotá D.C.
- Parques Nacionales Naturales de Colombia, 2016. Reformulacion Participativa Del Plan De Manejo Parque Nacional Natural Chingaza. Bogotá, Colombia.
- Parra-Romero, A., 2011. Análisis integral del conflicto asociado a la presencia del oso Andino (*Tremarctos ornatus*) y el desarrollo de sistemas productivos ganaderos en áreas de amortiguación del PNN Chingaza. Pontificia Universidad Javeriana. <https://doi.org/10.1017/CBO9781107415324.004>
- Parra-Romero, A., Galindo-Tarazona, R., González-Maya, J.F., Vela-Vargas, I.M., 2019a. Not eating alone: Andean bear time patterns and potential social scavenging behaviors. *Therya* 10, 49–53. <https://doi.org/10.12933/therya-19-625>
- Parra-Romero, A., Raigozo, E., Galindo-Tarazona, R., 2017. Estado de conservación y amenazas del oso andino en el macizo de Chingaza, in: González-Maya, J.F., Galindo-Tarazona, R., Urquijo-Collazos, M.M., Zárate-Vanegas, M., Parra-Romero, A. (Eds.), *El Oso Andino En El Macizo de Chingaza*. Bogotá D.C., p. 119.
- Parra-Romero, A., Zamudio-López, J., Camargo-Cardenas, J., Palacios-Medina, C., Torres, L., Castro, E., Espíndola, J., Menses, H., Vera-Villamizar, L., Moreno-Gutiérrez, S., López-Velandia, O., Saénz, F., Rodríguez, M., Franco, N., Clavijo-Rios, C., Rivera-Torres, C., López-Orjuela, H., Pachón-Bejarano, A., Jiménez-Palomo, G., Gutiérrez-Cuesta, F., Ayala-Cuchivaguen, J., Beltrán-Vergara, D., Marquéz, R., PNN de, C., Car, C., CORPOBOYACÁ, Corporinoquia, Corpochivor, Cormacarena, Corpoguavio, ABCA, WCS, 2019b. Ocupación del oso andino (*Tremarctos ornatus*) en la región centro-norte de la cordillera oriental de Colombia. Bogotá, Colombia.

- Pedraza, S., Sanchez, A., Clerici, N., Ospina, L., Quintero, A., Escobedo, F.J., 2020. Perception of conservation strategies and nature's contributions to people around Chingaza National Natural Park, Colombia. *Environ Conserv* 47, 158–165. <https://doi.org/10.1017/S037689292000020X>
- R TEAM DEVELOPMENT CORE, 2008. R: A language and environment for statistical computing.
- Redpath, S.M., Bhatia, S., Young, J., 2015. Tilting at wildlife: reconsidering human-wildlife conflict. *Oryx* 49, 222–225. <https://doi.org/10.1017/S0030605314000799>
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and Ecological Effects of the World's Largest Carnivores. *Science* (1979) 343, 1241484–1241484. <https://doi.org/10.1126/science.1241484>
- Rodríguez-Páez, S.A., Reyes-González, L., Rodríguez-Alvarez, C., González-Maya, J.F., Vela-Vargas, I.M., 2016. El Oso Andino guardián de los bosques. Gobernación de Cundinamarca, Parque Jaime Duque, Bogotá.
- Sánchez-Mercado, A., Ferrer-Paris, J.R., Yerena, E., García-Rangel, S., Rodríguez-Clark, K.M., 2008. Factors affecting poaching risk to Vulnerable Andean bears *Tremarctos ornatus* in the Cordillera de Merida, Venezuela: space, parks and people. *Oryx* 42, 437–447. <https://doi.org/10.1017/S0030605308006996>
- Soto, J.R., Adams, D.C., Escobedo, F.J., 2016. Landowner attitudes and willingness to accept compensation from forest carbon offsets: Application of best-worst choice modeling in Florida USA. *For Policy Econ* 63, 35–42. <https://doi.org/10.1016/j.forpol.2015.12.004>
- Toncheva, S., Fletcher, R., 2021. From Conflict to Conviviality? Transforming Human–Bear Relations in Bulgaria. *Frontiers in Conservation Science* 2. <https://doi.org/10.3389/fcosc.2021.682835>
- van Eeden, L., Eklund, A., Miller, J., López-Bao, J.V., Chapron, G., Cejtin, M.R., Crowther, M.S., Dickman, C.R., Frank, J., Krofel, M., Macdonald, D.W., McManus, J., Meyer, T.K., Middleton, A.D., Newsome, T.M., Ripple, W.J., Ritchie, E.G., Schmitz, O.J., Stoner, K.J., Tourani, M., Treves, A., 2018. Carnivore conservation needs evidence-based livestock protection. *PLoS Biol* 16, 1–8. <https://doi.org/10.1371/journal.pbio.2005577>
- van Eeden, L.M., Crowther, M.S., Dickman, C.R., Macdonald, D.W., Ripple, W.J., Ritchie, E.G., Newsome, T.M., 2018. Managing conflict between large carnivores and livestock. *Conservation Biology* 32, 26–34. <https://doi.org/10.1111/cobi.12959>
- Vargas Rios, O., Pedraza, P., 2004. Parque Nacional Natural Chingaza. Gente Nueva Era Editorial, Bogotá, Colombia.
- Vela-Vargas, I.M., Jorgenson, J.P., González-Maya, J.F., Koprowski, J.L., 2021. *Tremarctos ornatus* (Carnivora: Ursidae). *Mammalian Species* 53, 78–94. <https://doi.org/10.1093/mspecies/seab008>
- Velez-Liendo, X., Garcia-Rangel, S., 2017. *Tremarctos ornatus* [WWW Document]. The IUCN Red List of Threatened Species 2017.
- White, J.P., Stiver, W.H., Steinberg, M.K., Cissell, J.R., 2022. Comparing management techniques used on conflict American black bears in Great Smoky Mountains National Park. *Ursus* 2022. <https://doi.org/10.2192/URSUS-D-21-00008.R>
- White, P.C.L., Jennings, N.V., Renwick, A.R., Barker, N.H.L., 2005. Questionnaires in ecology: A review of past use and recommendations for best practice. *Journal of Applied Ecology* 42, 421–430. <https://doi.org/10.1111/j.1365-2664.2005.01032.x>

- Young, J.C., Marzano, M., White, R.M., McCracken, D.I., Redpath, S.M., Carss, D.N., Quine, C.P., Watt, A.D., 2010. The emergence of biodiversity conflicts from biodiversity impacts: Characteristics and management strategies. *Biodivers Conserv* 19, 3973–3990. <https://doi.org/10.1007/s10531-010-9941-7>
- Zimmermann, A., McQuinn, B., Macdonald, D.W., 2020. Levels of conflict over wildlife: Understanding and addressing the right problem. *Conserv Sci Pract* 2:e259, 1–8. <https://doi.org/10.1111/csp2.259>
- Zukowski, B., Ormsby, A., 2016. Andean Bear Livestock Depredation and Community Perceptions in Northern Ecuador. *Human Dimensions of Wildlife* 21, 111–126. <https://doi.org/10.1080/10871209.2015.1126871>
- Zuur, A.F., Gende, L.B., Ieno, E.N., Fernández, N.J., Eguaras, M.J., Fritz, R., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Modelling Applied on American Foulbrood Affecting Honey Bees Larvae, in: *Mixed Effects Models and Extensions in Ecology with R*. Springer New York, New York, NY, pp. 447–458. https://doi.org/10.1007/978-0-387-87458-6_19

Figure list

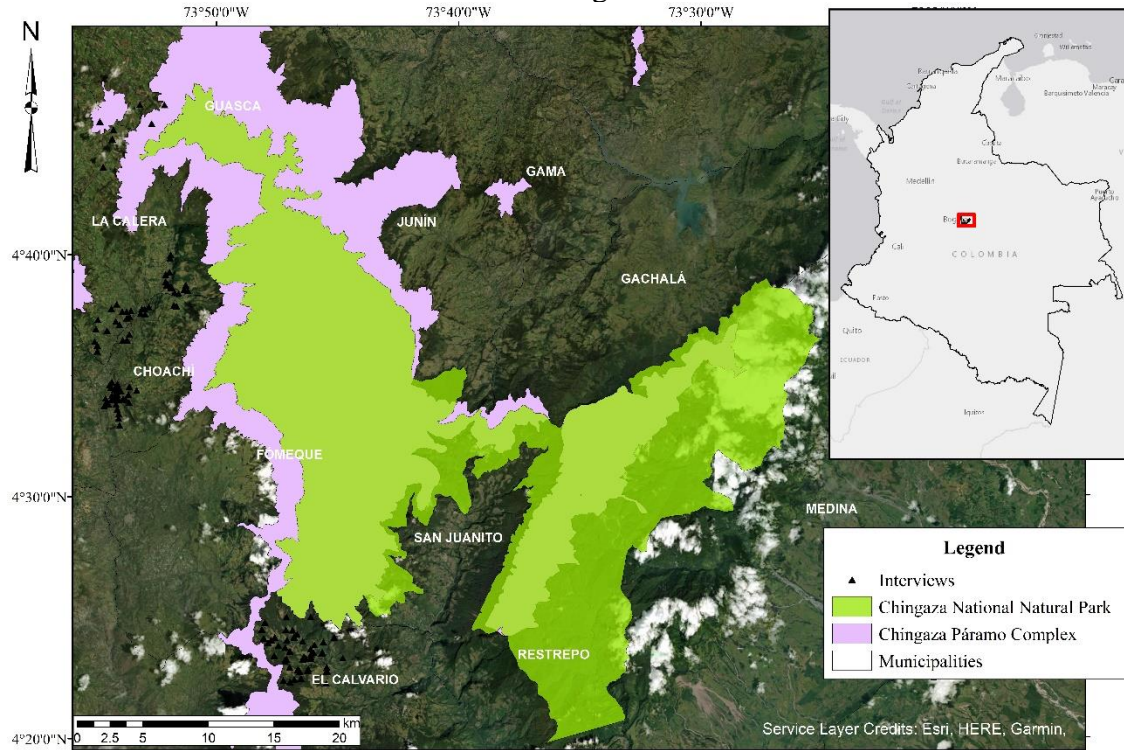


Figure 10. Study area and interviews performed at the Chingaza Massif, Colombia.

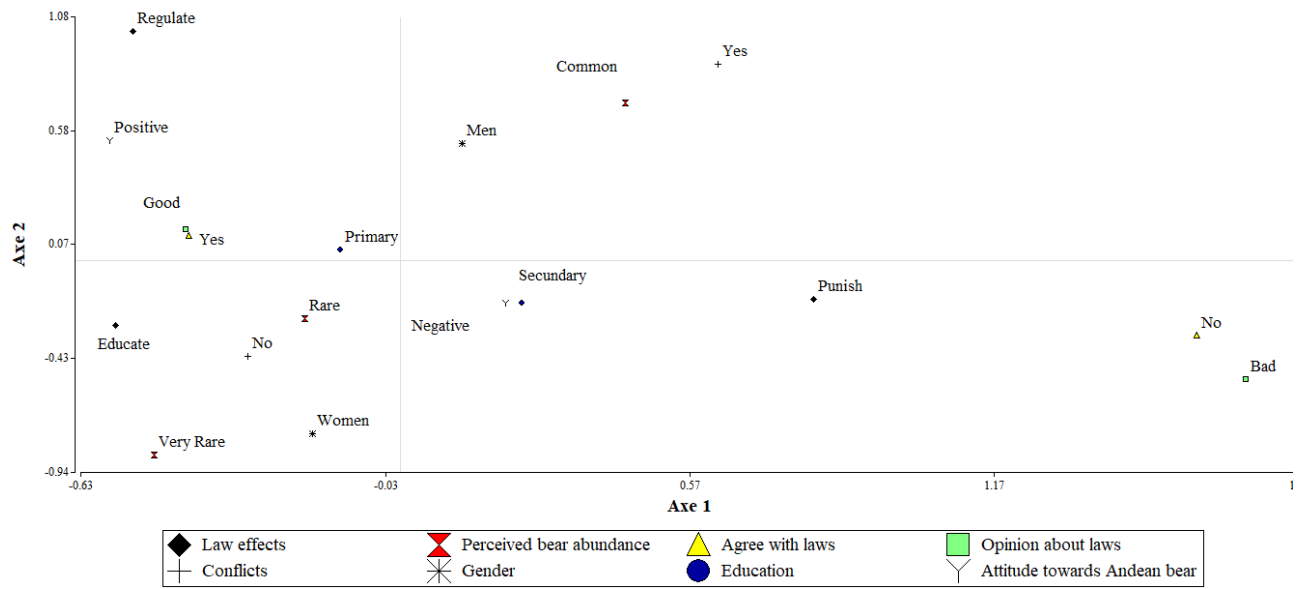


Figure 11. Correspondence analysis for attitudes towards Andean bear at the Chingaza Massif, Colombia

Table List

Table 4. Attributes and levels used to create the hypothetical scenarios.

Attribute	Description	Levels
Type of payment	Hypothetical scenario of retribution	Payment per Ha
		Payment per lost animal
Farm Area	Area of the farm that the rancher is willing to offer	< 5%
		> 5%
Time	Commitment period	< 2 years
		> 2 years
Implementer	Type of organization that perform monitoring of the program	NGO
		Government agency
Compensation*	Compensation for committed ha/farm	USD\$12
		USD\$37
		USD\$62
		USD\$87
	Payment for attacked cattle	USD\$68
		USD\$87
		USD\$111
		USD\$136

* US\$1= COP\$3693; COP is Colombian pesos (average rate during 2020)

Table 5. Ranking of the generalized linear models ($\Delta AIC < 2$) and average model for the evaluation of Human-Andean Bear Conflict (HABC) on the Chingaza Massif, Colombia.

RANKED MODELS ¹	AIC ²	ΔAIC ²	AICW ⁴
HUMAN – ANDEAN BEAR CONFLICTS			
VIGILANCE	137.94	0	0.40
VIGILANCE, AGE	139.92	1.97	0.14
NULL MODEL	156.40	18.45	3.95e ⁻⁵
AVERAGE MODEL FOR HUMAN – ANDEAN BEAR CONFLICTS			
VARIABLE	ESTIMATE ±SE	95% CI	
INTERCEPT	-1.1669± 0.8020	-2.9729 – 0.6390	
VIGILANCE (YES)	1.5989 ±0.8563 (.)	0.4953 – 0.7393	
VIGILANCE (NO)	-0.3784±0.8673	-2.0957– -1.3389	
AGE	-0.0852±0.2137	-0.0339 – 0.0225	

¹ Vigilance: Vigilance of cattle (presence/absence); Age: interviewee's age; Gender (Male/Female).

² Akaike information criterion for small samples.

³ Difference in AICc from best performing model.

⁴ Model weight estimate from the AICc.

(**), (*), (.) represent 0.01, 0.05, 0.1 level of statistical significance, respectively.

Table 6. Ranking of the generalized linear models ($\Delta AIC < 2$) and average model for the evaluation of Human-Andean Bear perceptions towards Andean bear on the Chingaza Massif, Colombia.

PERCEPTION TOWARDS ANDEAN BEARS			
RANKED MODELS ¹	AIC ²	ΔAIC ³	AICw ⁴
HABC	142.04	0	0.14
NULL MODEL	142.44163	0.39	0.12
HABC, PERCEIVED ABUNDANCE OF BEARS	143.44	1.39	0.07
HABC, ONWERSHIP	143.65	1.60	0.06
HABC, AGE	1243.72	1.67	0.06
AVERAGE MODEL FOR HUMAN PERCEPTION TOWARDS ANDEAN BEAR			
VARIABLE	ESTIMATE \pm SE	95% CI	
INTERCEPT	-0.8837 \pm 0.3476(*)	-1.3313 – -0.4361	
CONFLICT (YES)	-0.8075 \pm 0.5085	-1.4627 – -0.1523	
PERCEIVED ABUNDANCE (RARE)	-0.2210 \pm 0.5769	-0.9645 – 0.5224	
PERCEIVED ABUNDANCE (COMMON)	0.6123 \pm 0.5952	-0.1548 – 1.3794	
GENDER (MALE)	0.3074 \pm 0.4369	-0.2556 – 0.8705	
OWNERSHIP YEARS	-0.0072 \pm 0.1111	-0.021 – 0.0071	

¹ HABC: Human Andean Bear conflict (Presence/absence); Perceived abundance of bears: categories of perceived abundance of bears; Gender (Male/Female) Age: interviewee's age; Ownership: years of ownership of the farm.

² Akaike information criterion for small samples.

³ Difference in AICc from best performing model.

⁴ Model weight estimate from the AICc.

(**), (*), (.) represent 0.01, 0.05, 0.1 level of statistical significance, respectively.

Table 7. Random effects model estimation for Willingness to Accept (WTA) at the Chingaza Massif, Colombia.

VARIABLE	ESTIMATE ± SE	95% CI
INTERCEPT	4.1139e-01 ± 7.09e-02 (**)	2.72 e ⁻¹ – 5.50e ⁻¹
TYPE OF PAYMENT (HA/FARM)	6.3291e-02 ± 3.61e-02 (.)	-7.51e ⁻³ – 1.34e ⁻¹
FARM AREA < 5 HA	-6.3291e-02 ± 3.61e-02 (.)	-1.34e ⁻¹ – 7.54 e ⁻³
COMMITMENT PERIOD < 2 YEARS	-6.9620e-02 ± 2.90e-02 (*)	-1.26 x10 ⁻¹ - -1.26e ⁻¹
IMPLEMENTER (NGO)	-1.075e-01 ± 3.61e-02 (**)	-1.78 e ⁻¹ - -3.67e ⁻²
COMPENSATION (\$)	6.3291e-07 ± 1.75e-07 (**)	2.89e ⁻⁷ – 9.76e ⁻⁷