Therya

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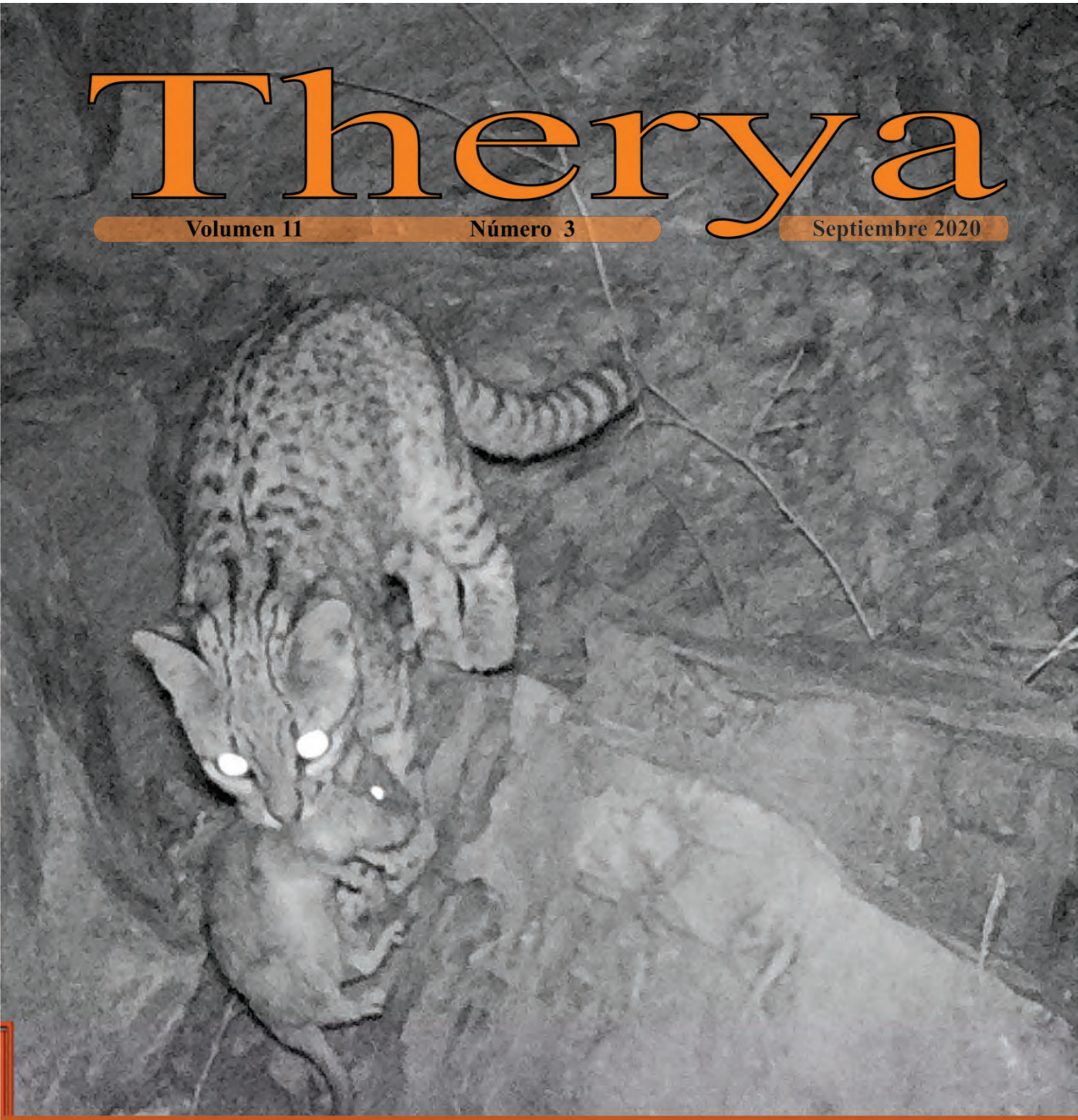

AMMAC

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La Portada

La rata chinchilla boliviana (*Abrocoma boliviensis*) es una de las especies de mamíferos más amenazadas del mundo. Esta foto, resultado de varios años de trabajo de campo, muestra un individuo, posiblemente hembra, siendo presa de un gato de Geoffroy. *A. boliviensis* fue descrita por William Glanz y Sydney Anderson en 1990, sin embargo, hasta el momento, la información científica sobre la especie es virtualmente inexistente. En este número de THERYA, con artículos dedicados a la memoria del Dr. Sydney Anderson, se presenta un trabajo dedicado a la ecología de *A. boliviensis* que muestra que todavía hay poblaciones de la especie, al parecer más o menos saludables, en el centro de Bolivia (fotografía: Carmen Julia Quiroga).

Nuestro logo "Ozomatli"

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

Therya

Volumen 11, número 3 septiembre 2020

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Therya

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

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Editorial

La enfermedad hemorrágica viral del conejo impacta a México y amenaza al resto de Latinoamérica

A través de boletines emitidos por el Servicio Geológico de los Estados Unidos (USGS - United States Geological Survey) y el Departamento de Agricultura de Estados Unidos (USDA - United States Department of Agriculture), se confirmó el 13 de abril de 2020, la reaparición de la enfermedad hemorrágica viral del conejo (RHDV Rabbit Hemorrhagic Disease Virus) con la presencia del serotipo RHDV2 (Rabbit Hemorrhagic Disease Virus Serotype 2) en liebres (*Lepus*), conejos domésticos (*Oryctolagus cuniculus*) y silvestres (*Sylvilagus, Romerolagus*), incluso provocando alerta respecto a las pikas (*Ochotona*; Cima 2020). Hasta donde se conoce, esta enfermedad no es zoonótica, esto es, no se transmite de fauna silvestre a los humanos y tampoco tiene relación con el SARS-CoV-2, causante del COVID-19 u otro virus de afectación respiratoria en humanos. Las muertes de conejos (hasta 1,000 individuos) han ocurrido en varios condados de los estados de Arizona, California, Colorado, Nevada, Nuevo México y Texas en Estados Unidos. En México se reportaron eventos concurrentes de RHDV (no confirmados con pruebas de laboratorio) en la liebre de cola negra (*Lepus californicus*) y el conejo del desierto (*Sylvilagus audubonii*) en los municipios de Jiménez, Ahumada y Allende, en Chihuahua (Sleeman 2020). El 17 de abril, la Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) confirmó la reaparición del RHDV. El llamado lo hizo a las Unidades de Manejo para la Conservación de la Vida Silvestre (UMAs) del país y pidió al público reportar al Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria (SENASICA) la información necesaria en caso de detectar ejemplares sospechosos de tener la enfermedad.

A inicios de marzo de 2020, los autores (ALT y JAF) recibimos reportes de rancheros y propietarios de tierras en Sonora y Chihuahua el registro de muerte de conejos y liebres silvestres sin causa aparente. El 14 de marzo, The Arizona Game and Fish Department anunció que el RHDV2 había matado liebres y conejos silvestres en ese estado norteamericano. El pasado 3 de abril de 2020, se notificaron conejos domésticos muertos en un predio del municipio de Nuevo Casas Grandes, en Chihuahua, situación que fue atendida por SENASICA. La historia clínica de los conejos fue por muerte súbita y hemorragia nasal. El predio fue despoblado de otros conejos y desinfectado en su totalidad porque existía relación epidemiológica (SENASICA 2020a). SENASICA envió muestras de órganos de hígado y bazo de conejos domésticos al laboratorio de salud animal de la Comisión México-Estados Unidos certificado como nivel tres de bioseguridad. Posteriormente, se evaluaron también muestras similares de liebres y se confirmó la presencia de la enfermedad hemorrágica viral en estos organismos. Sin embargo, aún hace falta que se determine científicamente la identidad taxonómica a nivel de las especies silvestres afectadas en México.

Hasta el momento, conocemos que han sido afectados por el RHDV2: el conejo europeo doméstico (*Oryctolagus cuniculus*) hasta con 50 individuos muertos en granjas ubicadas en el norte de Chihuahua; además de las especies silvestres cuya identidad es necesario verificar (*e. g.*, *S. audubonii*, *S. floridanus* y *L. californicus*) que han sido encontradas muertos en varios sitios del noreste y centro-sur de Durango, norte de Chihuahua, centro de Sonora, suroeste de Coahuila, norte de Baja California Sur y noroeste de Baja California (SENASICA 2020b; Figura 1; Tabla 1), donde se encontraron de 2 a 50 individuos muertos cada semana durante marzo. Hubo comunicación con las asociaciones locales de ganaderos para informarles sobre el manejo básico de los cadáveres y de la necesidad de notificar la situación a SENASICA.

La enfermedad hemorrágica viral del conejo. Es una enfermedad viral extremadamente contagiosa y a menudo mortal para los lagomorfos por el virus de la RHDV. La enfermedad es causada por un miembro del género *Lagovirus* y la familia Caliciviridae. El serotipo 2 o RHDV2 (identificado en Francia en 2010) tiene casi el 75-80 % de letalidad en un periodo de dos a tres días en animales a partir de 10-15 días de edad. La muerte es el resultado de una disfunción circulatoria generalizada asociada con coagulación intravascular diseminada y lesiones de hepatitis necrotizantes, el hígado se considera el sitio principal de replicación del virus (Ahmad *et al.* 2011). A menudo, no se observan signos de la enfermedad hasta que se presenta la muerte súbita y la nariz manchada de sangre, causada por una hemorragia interna asociada con necrosis hepática. Los lagomorfos infectados también pueden desarrollar fiebre, pierden el apetito, se muestran nerviosos o tienen respiración agitada, resultado de pulmones congestionados y edematosos (USDA y Animal and Plant Health Inspection Service 2019).

Aunque se desconoce el origen del RHDV, se cree que pudo haber surgido de calicivirus que circulan de forma asintomática en conejos europeos (*O. cuniculus*). El primer brote conocido de la enfermedad hemorrágica viral del conejo ocurrió en China en 1984, aparentemente propagado por conejos europeos, variedad angora, que habían sido importados de Europa (The Center for Food Security and Public Health *et al.* 2016). Posteriormente, se presentó en Corea en 1987 y se diseminó en Europa en 1988. El primer brote de RHDV reportado en el hemisferio occidental, ocurrió en México en 1988,

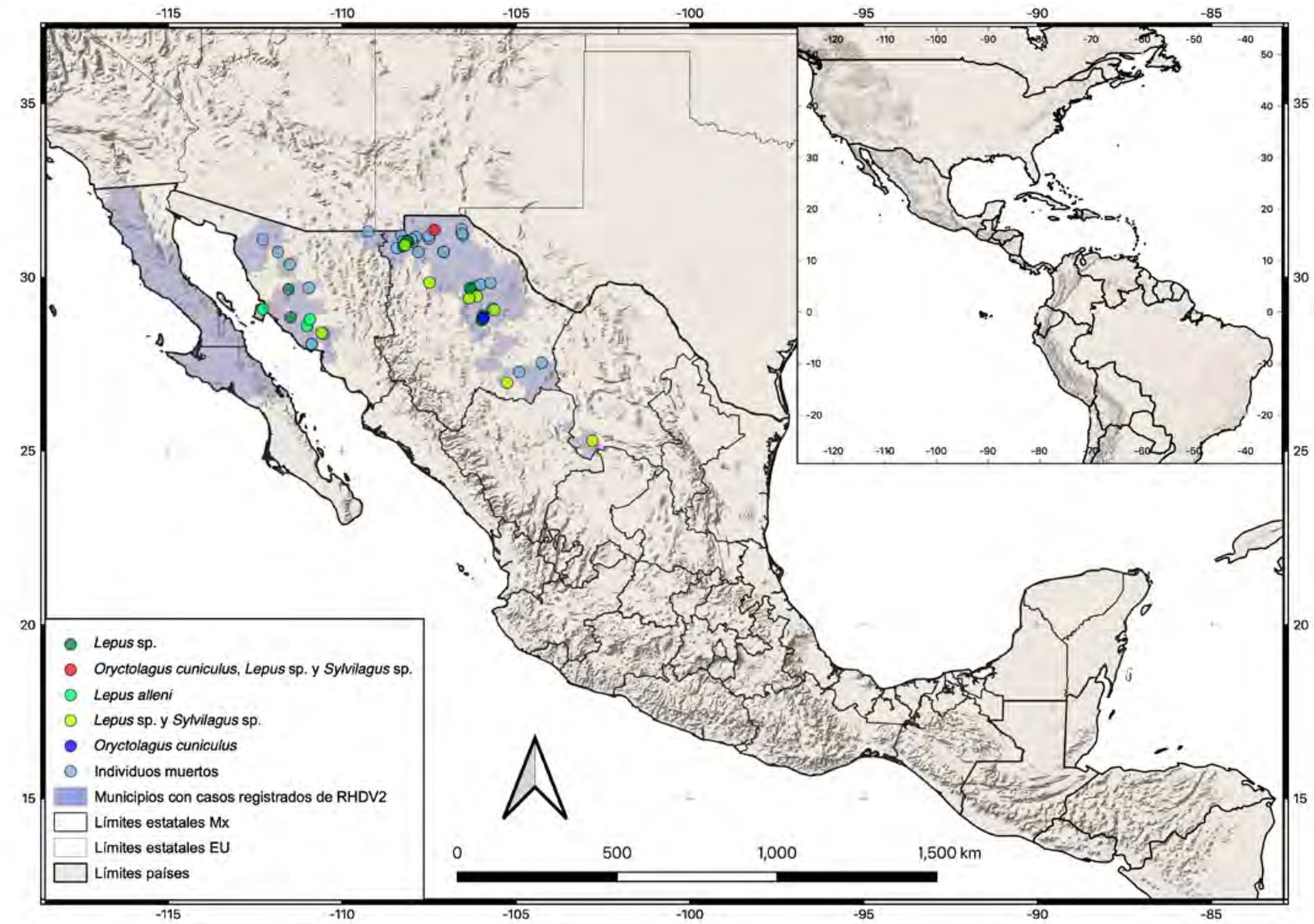

Figura 1. Registros de conejos domésticos y silvestres y liebres afectados por el RHDV2 en México. Se identifican las serranías en color gris obscuro.

provocado por la importación ilegal de canales de conejo originaria de China vía los Estados Unidos. La enfermedad se detectó en Cuba, en mayo de 1993 y en los Estados Unidos en abril de 2000, países que han sufrido reapariciones de la enfermedad en varias ocasiones (SENASICA 2020a). A inicios de este siglo, la enfermedad RHDV tuvo una distribución geográfica casi mundial (McIntosh *et al.* 2007). Actualmente, se teme que la presencia del serotipo RDHV2 se pueda dispersar hacia el resto de Latinoamérica.

El virus RHDV2 es muy resistente a temperaturas extremas. Se puede transmitir a través de las canales de conejos domésticos destinadas al consumo humano, a través de contacto directo o por la exposición a las excreciones y secreciones o sangre de un conejo infectado. El virus también puede sobrevivir y propagarse a partir de cadáveres y su consumo por depredadores o carroñeros, al consumir alimentos, agua y cualquier material contaminado. Las personas pueden transmitir el virus indirectamente al portarlo en ropa y zapatos (USDA y Animal and Plant Health Inspection Service 2019).

Para evitar la propagación de la enfermedad se indica usar equipo de protección personal y descontaminar todo el equipo de campo, la ropa y los vehículos. Además, evitar las necropsias de campo y, en su lugar, se recomienda recoger los cadáveres por completo y transportarlos a un laboratorio de contención apropiado para realizarla. Los cadáveres que no sean sometidos a necropsia deben ser incinerados o enterrados profundamente para impedir el acceso de animales carroñeros y la contaminación ambiental, ya que el virus podría propagarse nuevamente por las moscas o en las heces de los depredadores (SENASICA 2020a).

Importancia y efecto de la enfermedad hemorrágica viral del conejo en México, Centroamérica y Sudamérica

A medida que se acumularon casos reportados y basados en informes del suroeste de los Estados Unidos (Arizona, California, Colorado, Nevada, Nuevo México y Texas), surgieron preocupaciones sobre la salud de las granjas de conejos europeos y de ejemplares de razas exóticas mantenidas como mascotas, pero también acerca de las poblaciones de otros lagomorfos silvestres, debido a que el virus está afectando a las especies nativas. La presencia en el medio natural de las poblaciones de lagomorfos es básica, ya que, por su abundancia, son un elemento fundamental del delicado balance en las cadenas tróficas, tanto en su papel como consumidores primarios, así como de presas. Su desaparición parcial o total tendría consecuencias

Tabla 1. Localidades donde se ha detectado la enfermedad hemorrágica viral del conejo en México. * = Conejos domésticos y/o silvestres.

Estado	Municipio	Sitio/Predio	Latitud	Longitud	Especies
Baja California	Ensenada	No determinado	No determinada	No determinada	Conejos*
Baja California	Ensenada	No determinado	No determinada	No determinada	Conejos*
Baja California	Ensenada	No determinado	No determinada	No determinada	Conejos*
Baja California	Ensenada	No determinado	No determinada	No determinada	Conejos*
Baja California	Tecate	No determinado	No determinada	No determinada	Conejos*
Baja California Sur	Mulegé	No determinado	No determinada	No determinada	Conejos*
Chihuahua	Ascensión	Cerros Prietos	30°43´49.9”	107°05´02.2”	Individuos muertos
Chihuahua	Ascensión	El Chamizo	31° 27´ 14.8”	-107° 31´ 28.8”	Individuos muertos
Chihuahua	Ascensión	El Fresnal	31°06´57.9”	107° 29´54.0”	Individuos muertos
Chihuahua	Ascensión	Ejido Ascensión	31°09´43.3”	107°52´37.3”	Individuos muertos
Chihuahua	Ascensión	Ejido Los Reyes	31°03´15.6”	108°08´23.0”	Individuos muertos
Chihuahua	Ascensión	Laguna de Guzman	No determinada	No determinada	Individuos muertos
Chihuahua	Ascensión	La Cruz	31°01´00.2”	108°06´03.6”	*Lepus* spp.
Chihuahua	Ascensión	La Morita	31°00´55.4”	107°59´06.9”	Individuos muertos
Chihuahua	Ascensión	Rancho Las Lilas	30°55´39.0”	108°11´22.9”	*Lepus* spp. y *Sylvilagus* spp.
Chihuahua	Ascensión	Ranchos Tres Papalotes	31°12´01.8”	108°17´46.4”	Individuos muertos
Chihuahua	Ascensión	Ranchos varios	31°21´47.7”	107°20´53.1”	*Oryctolagus cuniculus*, *Lepus* spp. y *Sylvilagus* spp.
Chihuahua	Ascensión	Ranchos varios	3105´26.0”	108°00´04.0”	Individuos muertos
Chihuahua	Aldama	Brecha Norte	28°53´29.5”	105° 56´45.0”	*Lepus* spp.
Chihuahua	Aldama	El Morrión	29°03´37.0”	105° 37´24.7”	*Lepus* spp. y *Sylvilagus* spp.
Chihuahua	Aldama	El Venado	29°27´07.4”	106° 07´47.3”	*Lepus* spp. y *Sylvilagus* spp.
Chihuahua	Aldama	La Mesa	28°47´23.7”	105° 58´59.8”	*Lepus* spp.
Chihuahua	Aldama	Molina	28°46´19.0”	105° 58´59.8”	*Lepus* spp.
Chihuahua	Aldama	Zoológico	28°50´08.1”	105° 55´50.1”	*Oryctolagus cuniculus*
Chihuahua	Chihuahua	El Coyamito	29° 43´40.8”	106°09´02.9”	Individuos muertos
Chihuahua	Chihuahua	El Faro	29°23´49.5”	106° 20´58.3”	*Lepus* spp. y *Sylvilagus* spp.
Chihuahua	Chihuahua	El Quince	29°47´18.6”	106° 01´07.4”	Individuos muertos
Chihuahua	Chihuahua	La Gregoria	29°38´25.2”	106° 17´46.7”	*Lepus* spp.
Chihuahua	Chihuahua	La India	29°41´48.3”	106° 18´59.4”	*Lepus* spp.
Chihuahua	Coyame	Gemelos	29° 05´40.2”	105° 40´15.8”	Individuos muertos
Chihuahua	Coyame	Tres Castillos	29°50´15.5”	105°44¨10,5”	Individuos muertos
Chihuahua	Janos	Camino a Buenavista	31°02´12.5”	108°15´01.7	Individuos muertos
Chihuahua	Janos	El Uno	30°50´16.5”	108°25´38.2”	Individuos muertos
Chihuahua	Janos	La Cruz	31°02´36.1”	108°08´43.5”	*Lepus* spp.
Chihuahua	Janos	La Pradera	30°53´13.3”	108°14´39.4”	*Lepus* spp.
Chihuahua	Jimenez	Huerta Nogalera	27° 16´39.4”	104° 54´35.0”	Individuos muertos
Chihuahua	Jimenez	La Chavinda	27° 32´30.1”	104° 15´26.3”	Individuos muertos
Chihuahua	Juárez	Ojo de En medio	31° 22´ 50.4”	106° 33´45.0”	Individuos muertos
Chihuahua	Juárez	Rancho de Gonzalez	31° 12´24.6”	106° 31´23.4”	Individuos muertos
Chihuahua	Juárez	Rancho Jose Corral	31° 15´ 05.7”	106° 33´12.4”	Individuos muertos
Chihuahua	Meoqui	No determinado	No determinada	No determinada	Conejos*
Chihuahua	Nuevo Casas Grandes	Palma Alta	30° 43´ 37.0”	107° 48´23.9”	Individuos muertos
Chihuahua	San Buenaventura	Huertas	29°50´54.4”	107° 29´17.6”	*Lepus* spp. y *Sylvilagus* spp.
Chihuahua	Saucillo	No determinado	No determinada	No determinada	Conejos*
Chihuahua	Valle de Allende	Varios Ranchos	26° 57´51.2”	105° 14´58.3”	*Lepus* spp. y *Sylvilagus* spp.
Chihuahua	Valle de Zaragoza	No determinado	No determinada	No determinada	Conejos*
Chihuahua	Villa Ahumada	Varios Ranchos	No determinada	No determinada	*Lepus* spp. y *Sylvilagus* spp.
Coahuila	Viesca	La Viesca	25°20´ 28”	102°48‘16”	*Lepus* spp. y *Sylvilagus* spp.

Continuación...

Tabla 1. Localidades donde se ha detectado la enfermedad hemorrágica viral del conejo en México. * = Conejos domésticos y/o silvestres.

Estado	Municipio	Sitio/Predio	Latitud	Longitud	Especies
Durango	Gómez Palacio	No determinado	No determinada	No determinada	Conejos*
Durango	Delicias	No determinado	No determinada	No determinada	Conejos*
Sonora	Agua Prieta	San Bernardino	31°19´18.5”	109°15´18.5”	Individuos muertos
Sonora	Altar	Municipio	30°43´33.0”	111°50´54,2”	Individuos muertos
Sonora	Carbo	No determinado	29°41´40.4”	110°57´52.8”	Individuos muertos
Sonora	El Arivaipa	No determinado	31°05´03.7”	112°17´09.8”	Individuos muertos
Sonora	Félix Gomez	No determinado	28°04´46.7”	110°52´28.8”	Individuos muertos
Sonora	Guaymas	No determinado	28°04´39.8”	110°52´23.3”	Individuos muertos
Sonora	Guaymas	El Represo	28°23´53.3”	110°35´31.1”	*Lepus* spp. y *Sylvilagus* spp.
Sonora	Guaymas	La Pintada	28°35´49.7”	111°00´48.0”	*Lepus alleni*
Sonora	Hermosillo	La Mina	28°47´15.8”	110°55´30.5”	*Lepus alleni*
Sonora	La Misa	No determinado	28°22´38”	110°31´53”	Individuos muertos
Sonora	Miguel Alemán	Rancho Escalante	28°50´58.11”	111°28´57.6”	*Lepus* spp.
Sonora	Región	No determinado	29°39´02.2”	111°32´34.7”	*Lepus* spp.
Sonora	Trincheras	La Esperanza	30°22´19.2”	111°30´36.6”	Individuos muertos
Sonora	Isla Tiburón	Zona noroeste	29°05´48.7”	112°16´18.8”	*Lepus alleni*

de alcances inimaginados en los procesos ecológicos de los ecosistemas, seguramente con impactos negativos muy importantes en las poblaciones de las especies que se alimentan de lagomorfos y por tanto dependen de ellas, como serpientes de cascabel (*Crotalus* spp.), gatos monteses (*Lyns rufus*), coyotes (*Canis latrans*) y diversas especies de aves de presa (Lorenzo *et al.* 2015), con efectos en cascada difíciles de anticipar.

Existen 63 especies de lagomorfos lepóridos en el mundo (Smith *et al.* 2018) y México es uno de los países con mayor riqueza, debido a que está compuesta por 14 especies: 9 conejos (8 del género *Sylvilagus* y 1 del género *Romerolagus*) y 5 liebres (del género *Lepus*). La preocupación por la presencia del RHDV2 crece por la afectación que puedan presentar sus poblaciones; principalmente aquellas especies vulnerables o en peligro de extinción, así como aquellas que presentan áreas de distribución restringida o se distribuyen en áreas de importancia para la biodiversidad. Por ejemplo, el conejo zacatuche (*Romerolagus diazi*) en el Eje Neovolcánico es de particular preocupación porque el gobierno mexicano lo enlista en peligro de extinción (Trujillo-Segura 2019) y la International Union for the Conservation of Nature (IUCN) lo clasifica en peligro (Velázquez y Guerrero 2019). Otro ejemplo relevante se ubica en el norte de México (Coahuila), donde puede encontrarse el conejo de las montañas Davis, *S. robustus*, el cual es vulnerable según la IUCN (Ruedas y Smith 2019). Por otra parte, en los desiertos de Chihuahua y Sonora se distribuye la liebre de costados blancos (*Lepus callotis*), clasificada como vulnerable (Brown y Smith 2019) y la liebre antílope (*Lepus alleni*), considerada en la categoría de preocupación menor (Lorenzo y Brown 2019).

En el escenario hipotético de que el brote epidémico del RHDV2 se desbordara de manera natural a otras especies de lagomorfos silvestres distribuidas en el centro y sur de México y sin considerar la posible transportación de conejos domésticos a otras regiones ni el desplazamiento humano, su efecto sería devastador, provocando una pérdida de grandes dimensiones en la diversidad de especies de lagomorfos por tratarse de un virus altamente infeccioso y resistente a cambios ambientales. El RHDV2 requiere infectar un hospedero natural para su supervivencia, por lo que la distribución de las especies podría indicar las posibles rutas de dispersión del virus, sobre todo aquellas en las que no existen barreras geográficas que eviten su paso.

Debido a lo anterior, consideramos que las posibles vías de dispersión del RHDV2 en México pueden ser la parte norte de las planicies costeras en sus vertientes Pacífico y Golfo, así como la Meseta Central de México (Figura 1). A través de la Planicie Costera del Pacífico se verían afectadas poblaciones de los conejos, *S. audubonii*, *S. floridanus* y *S. cunicularius* (al noroeste de su distribución) y las liebres *L. californicus* (en el extremo norte) y *L. alleni*. En la Planicie Costera del Golfo, afectaría a los conejos, *S. floridanus* y *S. gabbi* (en el extremo norte) y a las liebres, *L. californicus* y *L. altamirae* (en el extremo norte; Vargas *et al.* 2019). En la Meseta Central se verían afectadas poblaciones de los conejos *S. floridanus*, *S. audubonii* y *S. robustus* y las liebres *L. californicus* y *L. callotis*. El avance del virus podría ser más lento para alcanzar a las especies serranas y aisladas, como *R. diazi* y *S. insonus* (en Sierra Madre del Sur de Guerrero). En cuanto a la Península de Baja California, el Río Colorado y Sierra de Juárez al norte de Baja California, son una fuerte barrera para el paso del RHDV2 proveniente del continente en territorio mexicano. Sin embargo, puede llegar por el norte desde el estado de California en los Estados Unidos, en este caso las especies que pueden verse afectadas son los conejos *S. audubonii*, *S. bachmani* y la liebre *L. californicus*. La dispersión natural del virus hacia las especies y subespecies de lagomorfos silvestres que habitan en las islas del Golfo de California

(*S. bachmani mansuetus*, Isla San José; *L. alleni tiburonensis*, Isla Tiburón; *L. c. sheldoni*, Isla Carmen; *L. c. insularis*, Isla Espíritu Santo; *L. c. xanti*, Isla Cerralvo) y del Océano Pacífico mexicano (*S. graysoni*, Islas Marías; *L. c. magdalenae*, Islas Magdalena y Margarita), se esperaría que fuera muy baja debido a su aislamiento geográfico. Sin embargo, el contagio podría facilitarse por el transporte involuntario a través de la ropa y calzado de las personas, o por medio de depredadores como aves de presa, como se piensa que pudo haber ocurrido en la Isla Tiburón en abril y mayo de 2020.

En Guatemala existen sistemas montañosos que se extienden hacia la frontera con México (Chiapas) como la Altiplanicie Central (Macizo Central o Los Altos de Chiapas), que se desplaza por la parte central del estado y proviene de Guatemala (Sierra de los Cuchumatanes) o la Franja Volcánica que inicia cerca de la frontera con Chiapas por la vertiente del Pacífico y se extiende por el centro del país. Estas barreras, junto con el cierre del Istmo Centroamericano (hace 2 a 5 millones de años aproximadamente) fueron de gran importancia para filtrar la dispersión de varias especies de lagomorfos de norte a sur, como son las liebres cuyo límite de distribución sureña es el Istmo de Tehuantepec (con *L. flavigularis*) y, por tanto, no se encuentran en Centroamérica y Sudamérica. Sin embargo, algunos conejos pudieron migrar hacia al sur y son éstos los que podrían verse afectados por el RHDV2, como *S. brasiliensis*, que se encuentra hasta el norte de Argentina, *S. gabbi* hasta Colombia y *S. floridanus* hasta Colombia y Venezuela. Otras poblaciones de conejos llegaron a especiar y actualmente son endémicos y con distribución local en algunos países, *S. dicei* en Costa Rica, *S. andinus* en Perú, *S. varynaensis* en Venezuela y *S. tapetillus* en Brasil; son éstos los que pueden ser un foco de atención ante eventos de posibles brotes del RHDV2.

Exhorto

Consideramos que las líneas de investigación futuras que deben tomarse en cuenta para evitar en la medida de lo posible brotes del RHDV2 deben enfocarse en contener el paso del virus, evitando (como se ha hecho) la restricción de transportar conejos domésticos a otras regiones, para lo cual se requiere contar con datos y rutas sobre la importación, cría, o ambos, del conejo doméstico en diferentes países, con el fin de tener una idea del riesgo sanitario de introducción. Es de importancia evaluar la riqueza de los lepóridos en Latinoamérica para identificar zonas que podrían ser de alta preocupación y atención inmediata. Así como colaborar con diferentes sectores sociales y académicos nacionales y extranjeros para contar con registros precisos de fechas de aparición de brotes y llevar al cabo acciones conjuntas para su manejo y para evitar su dispersión.

Aunque en México existen programas de erradicación de RHDV en conejos domésticos desde 1989 por parte del Sistema Nacional de Emergencia en Salud Animal (SINESA), se requiere de información detallada recopilada en campo para evaluar variaciones en el tamaño de las poblaciones silvestres infectadas con el virus RHDV2. Por todo lo anterior, es fundamental la cooperación entre las autoridades gubernamentales, el sector académico y los habitantes locales para realizar trabajo de campo coordinado para implementar medidas de bioseguridad con el fin de contener la RHDV2 en poblaciones silvestres, ya que la propagación indirecta del virus es altamente efectiva.

Existen vacunas para RHDV2 para conejos domésticos; sin embargo, no están aprobadas para uso comercial en los Estados Unidos. Además, existe una protección cruzada limitada o nula entre los grupos de virus, es decir, que se debe elegir el tipo de vacuna de acuerdo con la variante de la que se busque inducir una reacción inmunogénica (SENASICA 2020a). No existen vacunas para las especies silvestres y si así fuera, su aplicación requeriría de un gran esfuerzo ya que los animales tendrían que atraparse, vacunarse y liberarse. Como en pasados eventos de pandemia de la enfermedad hemorrágica viral del conejo, es probable que, a partir de los sobrevivientes inmunes, se pueda obtener una inmunidad de la población después de un tiempo. Sin embargo, es necesario unir esfuerzos para enfrentar este reto que enfrenta la conservación y aprovechamiento sustentable de la biodiversidad y mitigar sus efectos que, finalmente sumado a otros eventos similares, incide sobre la supervivencia de la especie humana.

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Editorial

Papers in honor of Syd Anderson's contributions to Bolivian and Neotropical Mammalogy

The current issue of *Therya* includes a number of papers honoring the legacy and notable contributions of Dr. Sydney Anderson (1927-2018) to Bolivian and Neotropical mammalogy. "El Doc," as he was warmly referred to by hordes of Bolivians scientists and students, was as a towering example of an unassuming mammalogist who loved and honored his science so much that he enjoyed camping and trapping in remote areas of Bolivia for almost three decades, and until he was well into his late 60s.

His single-most important contribution to Bolivian and Neotropical mammalogy was his "Mammals of Bolivia, taxonomy and distribution" (Anderson 1997). This monumental monograph has been recognized as the fundamental pillar of contemporary Bolivian mammalogy *(e. g.*, Tarifa 2014). Significantly, in order to clarify issues such as species boundaries, distributions, and other aspects of taxonomy and systematics to be included in that monograph, Anderson and numerous collaborators published on several taxa also present in neighboring countries. See an overview of Syd's academic career and contributions in Gardner *et al.* (2020). We started planning this special contribution to *Therya* in mid 2019. At the time, the last draft of the updated and annotated checklist of the mammals of Bolivia (Aguirre *et al.* 2019) was circulating among the authors, and we had yet not heard of Anderson's passing. While completing that work, we could not fail to be impressed by the magnitude of Anderson's contributions to Bolivian mammalogy. When we learned of his death, we immediately began planning a Festschrift in his honor. We drafted an invitation and sent it to over 70 potential contributors in late 2019. We targeted several groups of authors, from people who had worked with him at the American Museum of Natural History to Latin American scientists who had directly worked with him over the many decades of his active career. People also were free to invite any potential collaborators. We received positive responses from about 55 potential contributors. Then, the COVID-19 pandemic happened and several promised manuscripts never materialized. We think Syd would have approved of selecting *Therya*, the official journal of the Mexican Mammal Society, as an ideal venue for the publication of this memorial for several reasons: Anderson's interest in and support for Latin American mammalogists, their societies, and their development were patent throughout his life. In addition, he published extensively on Mexican mammals. We are pleased with the selection of papers that are included in this special contribution as well as with the range of topics encompassed: we think they are a fitting homage to Anderson's efforts in the development of Bolivian and Neotropical Mammalogy.

Finally, we cannot close this editorial without mentioning Justine Anderson. Syd acknowledged her in his Mammals of Bolivia (Anderson 1997: 5) as "My wife, friend, field assistant, and photographer", but for those of us that spent time with them in the field (yes, Justine was there too!) it was clear that Syd and Justine were a team! Justine passed away early this year. We are proud to have known, worked, and learned so much from both of them.

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Sustained impact of holistic specimens for mammalogy and parasitology in South America: Sydney Anderson's legacy

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Sydney Anderson and the "Mammalian Diversity in Bolivia" (MDB) project (1984-1993) established a highly productive model for integrated specimen-based field expeditions. We assess the extended impact of that decade-long series of holistic surveys of mammalian diversity as a productive model for building enduring and highly integrated infrastructure for biodiversity research. We point to specific examples of impact, but more generally make a case for Sydney Anderson's prescient view that collections, over time, become ever more powerful and essential scientific tools for understanding mammalian diversity and our rapidly changing planet. To assess the number of specimens held in collections and their availability for spatial analyses, we queried the Global Biodiversity Information Facility (GBIF) for Bolivian specimens. Results were downloaded and non-georeferenced specimens were georeferenced in GeoLocate. Publications utilizing specimens or data from the MDB project were identified in Google Scholar, these were used to build a citation profile to analyze impact and breadth of research. Over the course of the decade-long MDB project ca. 10,000 new "holistic" specimens were added to natural history collections in Bolivia and the United States. These specimens and data were used in over 500 papers across a broad range of research areas, including new records for the country, and many descriptions of mammals (nine) and parasites (34) new to science. The Google Scholar profile generated for these publications has more than 20,000 citations and a citation H-index = 68 and an i-10 = 340. Sydney Anderson's legacy will endure through the exceptional collections he helped to build and the wide array of students he helped to inspire. As societal concerns related to environmental change (*e. g.*, biological annihilation, climate change, emerging zoonotic pathogens) become more pressing, scientific questions evolve, and technology continues to develop, these critical resources will be called upon more and more frequently. Thus we can confidently predict that the value and use of the Bolivian mammal specimens archived under Syd Anderson's leadership will continue to increase in the future.

Sydney Anderson y el proyecto "Diversidad de mamíferos en Bolivia" (MDB; 1984-1993) establecieron un modelo altamente productivo para expediciones integrales de campo basadas en muestras. Evaluamos el impacto extendido de esa serie de estudios holísticos de la década de la diversidad de mamíferos como modelo productivo para construir una infraestructura duradera y altamente integrada para la investigación de la biodiversidad. Se señalan ejemplos específicos del impacto, pero en general exponemos la visión premonitoria de Sydney Anderson respecto a que las colecciones, con el tiempo, se convertirán en herramientas científicas cada vez más poderosas y esenciales para comprender la diversidad de mamíferos y a nuestro planeta que cambia rápidamente. Para evaluar el número de especímenes almacenados en colecciones y su disponibilidad para análisis espaciales, consultamos el Global Biodiversity Information Facility (GBIF) para especímenes de Bolivia. Los resultados se descargaron y las muestras no georreferenciadas se georreferenciaron en GeoLocate. Las publicaciones con muestras o datos del proyecto MDB se identificaron en Google Scholar y se utilizaron para crear un perfil de citas, analizar el impacto y la amplitud de la investigación. En el transcurso de una década del proyecto de MDB se agregaron aproximadamente 10,000 nuevos especímenes "holísticos" a las colecciones de historia natural en Bolivia y los Estados Unidos. Estos especímenes y datos se utilizaron en más de 500 artículos referidos a una amplia gama de temas y áreas de investigación, incluyendo nuevos registros para el país y descripciones de mamíferos (9) y parásitos (34) nuevos para la ciencia. El perfil de Google Scholar generado para estas publicaciones tiene más de 20,000 citas y un índice de citación H = 68 y i-10 = 340. El legado de Sydney Anderson perdurará en el tiempo a través de las excepcionales colecciones que ayudó a construir y la amplia gama de estudiantes que ayudó a inspirar. . A medida que las preocupaciones sociales relacionadas con el cambio ambiental (por ejemplo, la aniquilación biológica, el cambio climático, los patógenos zoonóticos emergentes) se vuelven más acuciantes, las preguntas científicas evolucionan y la tecnología continúa desarrollándose, estos recursos críticos se recurrirán cada vez con mayor frecuencia. Por lo tanto, podemos predecir con confianza que el valor y el uso de los especímenes de mamíferos bolivianos bajo el liderazgo de Syd Anderson continuarán aumentando en el futuro.

Keywords: biodiversity infrastructure; Bolivia; mammals; natural history collection.

Introduction

"..… (I) have done what I could to encourage and expedite the work of others on these taxa, although it is frustrating, in a way, to leave so many of them unresolved."

(Sydney Anderson 1997, Mammals of Bolivia).

Despite his sentiment on leaving matters unresolved, there is little doubt that Sydney Anderson left a legacy that will not only endure, but grow, as the biodiversity infrastructure he helped build is used by generations of scientists to come.

Over a decade of fieldwork (1984-1993), the Mammalian Diversity in Bolivia (MDB) survey established a highly productive model for integrated specimen-based field expeditions. With funding from the National Science Foundation and under the leadership of Sydney Anderson (American Museum of Natural History, AMNH), Terry Yates and Joseph Cook (Museum of Southwestern Biology, University of New Mexico, MSB), and Scott Gardner (University of California-Davis, UCD and the Manter Laboratory of Parasitology, University of Nebraska, Lincoln, HWWL), this highly collaborative project involved a number of Bolivian institutions including the Colección Boliviana de Fauna in the La Paz (CBF), the Museo de Historia Natural "Noel Kempff Mercado" in Santa Cruz, Bolivia (MHNNKM), Centro Nacional de Enfermedades Tropicales (CENETROP), Zoofauna SudAmericana—Santa Cruz, Instituto Boliviano de Biología de la Altura, La Paz (IBBA), and Instituto de Ecología, Universidad Mayor de San Andrés (UMSA). The MDB represented the initiation of a more rigorous, comprehensive, and integrated methodology in specimen preparation, designed to encompass not just the mammal and its morphologic characters, but to also archive as broad a spectrum of tissues as possible, and with a dual focus on each mammal specimen's associated parasites. The traditional voucher (skin and skeleton-- Hafner *et al.* 1984, or fluid preserved specimen) was supplemented by an array of ultrafrozen tissues, chromosome cell suspensions, fecal samples, and endo and ectoparasites. Now termed the "Holistic Specimen" (Cook *et al.* 2016; Galbreath *et al.* 2019), but also known as the "Extended Specimen" (Webster 2017), these specimens provide a breadth of materials to address not only traditional systematic and taxonomic questions, but now facilitate and integrate questions in environmental change (*e. g.,* climate change, habitat conversion, pollutants and toxicants, biodiversity loss, introduction of exotics), and other novel and evolving contemporary research areas (*e. g.,* pathogen emergence and discovery, genomics, microbiomes, isotopic and molecular ecology, metagenomics, transcriptomics, and proteomics; Cook *et al.* 2017; Dunnum *et al.* 2017; Greiman *et al.* 2018; Schindel and Cook 2018).

The MDB project produced more than 10,000 holistic mammal specimens from diverse biomes throughout "el Corazón de Sudamérica". These materials are now deposited in the collections of the AMNH, CBF, MHNNKM, and MSB, along with thousands of lots of associated ectoparasites (*e. g.,* fleas, ticks, lice) and endoparasites (*e. g.,* helminths) that were deposited in the HWML. To date, those specimens and their related data have served as the basis for hundreds of publications and graduate theses. Many of those studies, in turn, have been highly cited, revealing how holistic mammalian surveys, if properly archived, can continue to produce diverse, integrated, novel perspectives on mammalian biology in this hyper-diverse region long after the initial field research is completed.

Collections serve as primary infrastructure for environmental science. Research questions using specimens today are often quite different from the original goals of specimen collection (McLean *et al.* 2016). The kinds of studies using samples and data from specimens have exploded (Pauli *et al.* 2017; Schmitt *et al.* 2018), yet sample availability for nearly all natural populations and species remains too limited (Malaney and Cook 2018). Sydney Anderson realized that building collections, essentially libraries of biodiversity, was key to ensuring their primary role in biodiversity sciences. Biodiversity sciences leverage this primary infrastructure in diverse ways. Herein, we point to how the integrated, holistic datasets uniquely offered by the Bolivian specimens have already improved understanding of geographic variation (*e. g.,* morphological, genomic, ecological), interactions among organisms (*e. g.,* host-parasite, host-microbiome, habitat), and the relationship between humans and wildlife health and will continue to do so well into the future. Multiple fields and scientific approaches can use this primary infrastructure and associated datasets to build and test hypotheses about natural and anthropogenically altered phenomena.

In addition to building scientific collections, the MDB survey combined with Sydney Anderson's engagement with Bolivian national, regional, and university-based museums provided exceptional cross-cultural opportunities for both Bolivian and North American students (the next generation of specimen-based scientists) to gain hands on experience in field mammalogy, parasitology, and museum curation.

Here, we assess the extended impact of that decade long series of holistic surveys of mammalian diversity as a productive model for building enduring and highly integrated infrastructure for biodiversity and human health. We point to specific examples of impact, but more generally make a case for Sydney Anderson's prescient view that collections, over time, become ever more powerful and essential scientific tools for understanding mammalian diversity and our rapidly changing planet.

Materials and methods

To assess the number of specimens held in collections and their availability for spatial analyses, we queried the Global Biodiversity Information Facility (GBIF) using the following parameters: Basis of record - "preserved specimen"; Country or area – "Bolivia"; Scientific name – "Mammalia". During the MDB survey, AMNH did not have frozen tissue storage facilities so all tissue samples and karyotypes were deposited at the MSB. Tissues from traditional voucher specimens (skin/skeleton/fluid specimens) held at the AMNH were cataloged as tissue only specimens at MSB and linked to the corresponding vouchers cataloged at AMNH though the Arctos collection management database (arctosdb.org). In GBIF this results in duplicate records for the same individual so for these analyses we removed duplicates. For those GBIF records without coordinate information, we georeferenced those with unambiguous localities using GeoLocate (http://www.museum.tulane.edu/geolocate/; Rios and Bart 2014).

To identify publications which utilized MDB specimens or data, we used Google Scholar searches based on a series of keywords (*e. g.,* Bolivia, mammal, MSB, AMNH, CBF, MNKM) and our knowledge of the material collected and loaned. This publication list was then used to accomplish two objectives: 1) assess the breadth of research for which MDB specimens contributed to, and 2) build a Google Scholar profile with citation indices to assess total impact.

Evaluation of the research content area was accomplished by assigning each publication to one of seven broad categories: 1) Systematics, taxonomy, and phylogeography, 2) New records/species distributions, 3) Taxon accounts in larger reference works, 4) Species compilations or keys, 5) Conservation and biogeography, 6) Parasite and pathogen biology and discovery, and 7) other areas.

Results and discussion

Impact on Bolivian natural history specimen growth. The beginnings of Bolivian mammalogical collections dates back to the early 1800's and continued sporadically into the early 1960's. Accurately accounting for all Bolivian specimens archived remains daunting due to incomplete digitization in the broad array of collections holding material, and was not attempted for this report. We estimate that no more than 5,000 specimens resulted from these early efforts documenting the country for the period 1818 through 1962. Tarifa (2014) and Anderson (1997) provide detailed overviews of the important events, people and institutions involved in the early years of Bolivian mammalogy. The ensuing decade (1960's) saw major projects focused on disease investigations related to a Bolivian hemorrhagic fever outbreak in the Beni region. These surveys by the Middle American Research Unit (MARU) and U. S. Army Medical Research and Development Command (USAMRD) generated large collections (ca. 13,000 specimens) now archived at the USNM, FMNH, and AMNH. The AMNH/USAMRD project led by Richard Van Gelder was Sydney's first foray into documenting Bolivian fauna and represents his first contributions to Bolivian mammalogy. Subsequently, from 1979-1983, Sydney (accompanied by his wife Justine) made various journeys to Bolivia to collect mammals (*ca*. 1,200 specimens) throughout the country. These trips would serve as the foundation for later expeditions with the CBF, MHNNKM, MSB, and HWWL (Anderson 1997). Over the course of the decade-long MDB survey about 10,000 new "holistic" specimens were preserved and added to museum collections (Table 1) and by the time he began work on "Mammals of Bolivia", he had access to about 36,000 specimens.

GBIF searches (GBIF.org; 19 April 2020) resulted in 36,249 records from 41 collections (GBIF Occurrence Download https://doi.org/10.15468/dl.rppf79) but that total includes specimens shared between MSB/AMNH. After removing duplicate records, 32,590 digitized specimens were available for analyses. Based on information provided in Anderson (1997) and Dunnum *et al.* (2018), we recognize there are also specimen records not available through GBIF and thus not reflected in the total, including the holdings of the four Bolivian natural history collections. Dunnum *et al.* (2018) reported a total of about 14,000 specimens from those collections: Museo de Historia Natural "Alcide d'Orbigny" (MHNC-M; 166 specimens), Colección de Fauna Centro de Biodiversidad y Genética (CCBG; 265 specimens), MHNNKM (5,200 specimens), and CBF (8,211 specimens). Thus, we estimate the total number of Bolivian specimens to approach 50,000, based on the combined GBIF data, un-digitized specimens held in other collections that we are aware of, and growth in collections since publication of Dunnum *et al.* (2018). Therefore, we estimate that there are approximately 0.045 specimens per km^2 collected in Bolivia (50,000/1.099 million km^2). About a third of the specimen records (12,015 specimens) in GBIF are not georeferenced, including much of the early collections by the Smithsonian (USNM), British Museum (NHMUK), and AMNH.

Table 1. Summary of expeditions from the Mammalian Diversity of Bolivia (MDB) survey (1984-1993).

Year	Locations (Department)	Approx. Specimens
1984	Oruro, Cochabamba, Beni, Santa Cruz	1,200
1985	Beni, Chuquisaca, La Paz, Santa Cruz	1,500
1986	Beni, Chuquisaca, La Paz, Oruro, Pando, Potosi, Tarija	1,300
1987	Santa Cruz	250
1988	Santa Cruz	700
1990	Chuquisaca, Santa Cruz	1,000
1991	Cochabamba, Santa Cruz, Tarija	1,770
1992	Beni, La Paz, Santa Cruz	770
1993	Beni, Cochabamba, La Paz	1,300

We (JLM) were able to georeference an additional 8,265 of those specimens to bring the total number to 28,834. Thus, we produced specimen heat maps (Figure 1) which included *ca.* 89 % of the specimens in GBIF, however, when also considering the specimens not available in GBIF, these analyses represent only about 60 % of the total Bolivian collections. This reduction in specimens for spatial analyses, reinforces the point that full value of specimens is only realized when they are properly georeferenced, digitized, and made available on-line. Thus, while patterns seen in these maps are largely accurate based on our knowledge of the primary areas of collection in Bolivia, inclusion of the material held in the Bolivian natural history collections would certainly refine the precision of the spatial distribution of specimen coverage.

From a temporal sampling perspective, there exist almost no areas where there is adequate sampling through time (Figures 1a to 1d), material and data absolutely vital to robustly assessing any type of environmental change. The forty-year period until 1963 (Figure 1a) illustrates the overall relatively low numbers of specimens, collected primarily from the central and eastern portions of the country, with nearly half the country devoid of any sampling. The period from 1963-1983 (Figure 1b) exemplifies the impact of disease related projects in northern and western lowlands as well as bat surveys in La Paz and Santa Cruz departments. However, the southern highlands were largely unsampled during those twenty

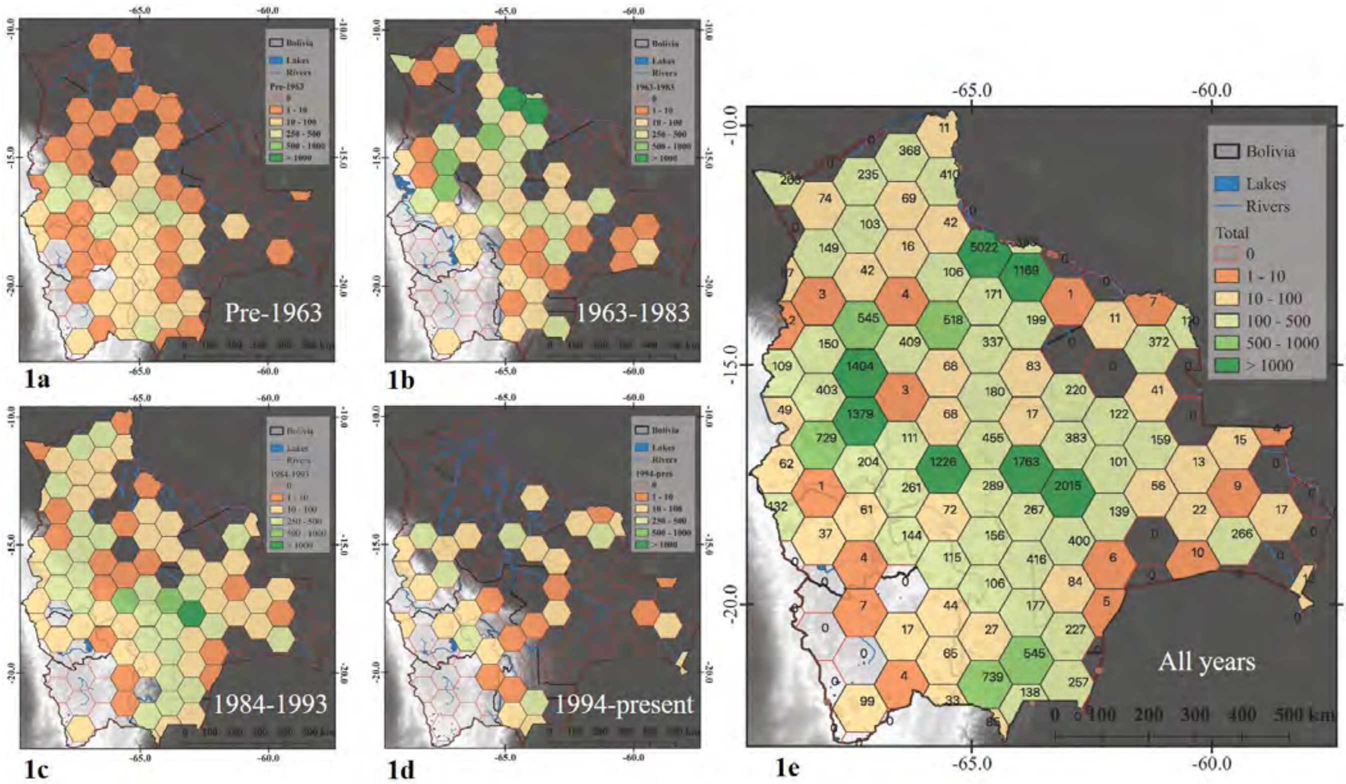

Figure 1. Heat maps of Bolivian specimens available on GBIF and containing georeferenced data: 1a) specimens collected prior to 1963. 1b) specimens collected between 1963-1983. 1c) specimens collected during the period of the Mammalian Diversity of Bolivia (MDB) survey (1984-1993). 1d) specimens collected from 1994 through the present. 1e) combined total specimens for all years with numeric value for each hexagon noted.

years. The decade of the MDB surveys (Figure 1c) saw a major increase in sampling across the country but most prominently along the eastern versant of the Andes. Despite only representing a single decade, the MDB survey era represents the period of greatest spatial coverage. Despite gains made during that period, based on these data there has been a reduction in sampling over the past 20 years (Figure 1d), a period of significant global climate change and environmental alternations. These numbers perhaps would not look quite as grim if specimens from the Bolivian natural history collections were included because many of those represent recently collected material but the general issue would remain.

Pooling all specimens through time (Figure 1e) shows that about 60 % of the country has < 100 specimens/hex (~10,000 km^2), including areas in the southern highlands and the Bolivian Chaco which are extremely depauperate of material. About 90 % of the areas within the country are represented by fewer than 500 specimens. The only areas with numbers over 1,000 are around the major urban centers of La Paz (2,783 specimens), Cochabamba (1,226 specimens), and Santa Cruz (3,778 specimens), and the BHF outbreak investigation area (6,191 specimens) in the Beni.

The take-home message remains that, like the majority of places on our planet, Bolivia remains vastly undersampled on both a spatial and temporal scale and there are many parts of the country which have already been irreparably altered through habitat conversion before they could be even partially documented. Large-scale funded projects like the MDB survey have the potential to make large contributions, but are unfortunately few and far between, thus broad spatial and temporal surveys of biodiversity need to be supported through diverse collaborations leveraging both in-country and global entities and resources.

Impact of Bolivian Specimen Infrastructure on Science. The MDB project developed new field-based protocols for preserving holistic specimens that would facilitate research that integrated across studies of hosts and parasites (Gardner 1996; Gardner and Jiménez-Ruiz 2009). These field techniques have been subsequently expanded and refined through other large sampling efforts worldwide with new cohorts of mammalogists and parasitologists (*e. g.,* Beringian Coevolution Project, Cook *et al.* 2017). From those efforts, best practices in holistic sampling of mammal and parasite faunas (Galbreath *et al.* 2019) now codify the concept of the holistic mammal specimen. Having now advocated for the concept of the "holistic specimens", it must be said that Sydney Anderson was a proponent of saving any piece of animal material he encountered on the roadways of Bolivia, no matter how flattened or degraded as it might be. He would wryly note each "road-kill record" would add another "vouchered dot" on the distribution map for a particular species. More than a few specimens were composed of nothing more than a patch of skin scraped from the roadway, carefully annotated with location and date of collection. In retrospect, those materials were important as they often represented a larger, poorly sampled carnivore and are now irreplaceable because technology has advanced to the point of allowing the extraction of genetic or isotopic signatures from extremely marginal material.

Sydney Anderson's years spent working in Bolivia and then reviewing the collections at MHNNKM, CBF, AMNH, or MSB produced many publications dealing with the distribution and systematics of this South American mammalian fauna (Anderson 1982, 1985, 1993, 1997; Anderson *et al.* 1982; Anderson and Olds 1989; Anderson *et al.* 1993; Anderson and Webster 1983; Anderson and Yates 2000; Anderson *et al.* 1987; Cook *et al.* 1990; Gardner and Anderson 2001; Glanz and Anderson 1990; Hinojosa *et al.* 1987; Olds and Anderson 1987, 1989; Olds *et al.* 1987; Salazar and Anderson 1990; Salazar *et al.* 1994). His monograph, "Mammals of Bolivia, Taxonomy and Distribution" (1997), has a place on every Neotropical mammalogist's bookshelf and has served as a vital resource for diverse research, public health, and wildlife management initiatives for three decades (670 citations). A growing body of subsequent works have built upon that foundational contribution.

Notwithstanding Sydney Anderson's published contributions to the systematics and taxonomy of Bolivia's mammalian fauna, his true Bolivian legacy may lie in the vast series of natural history specimens and associated data that he collected, compiled, organized, and curated over the decade he spent on this project. He was a seasoned and enthusiastic field mammalogist, even when setting his own traplines was no longer possible. He could always be counted on to finish preparing and check the work on all specimens. During the days, he would fastidiously monitor the progress on the drying skins and carcasses, often checking for maggots or mold, and moving the skeleton pile into direct sunlight or out of the rain. His catalog numbered in the 10,000's, and he took it upon himself to not only prepare massive numbers of specimens while in the field but to also carefully document the activities of the day and the localities visited (Figure 2). Much of what he recorded would eventually make it into various accounts on Bolivian fauna, including his book "Mammals of Bolivia". The collections from the MDB survey also have fostered a wide array of research on mammals and associated parasites.

A series of Google Scholar searches identified over 500 papers that used specimens or associated data from the MDB survey (Figure 3). It should be noted that only 49 of these papers were published during the life of the NSF grants, suggesting that the long-term value of specimen-based initiatives continue to generate value, as well as integrate knowledge across scientific fields, long after the grant cycle has concluded.

Figure 2. Syd Anderson writing fieldnotes and tending to drying specimens (Rio Aceromarca, La Paz Department, 1991).

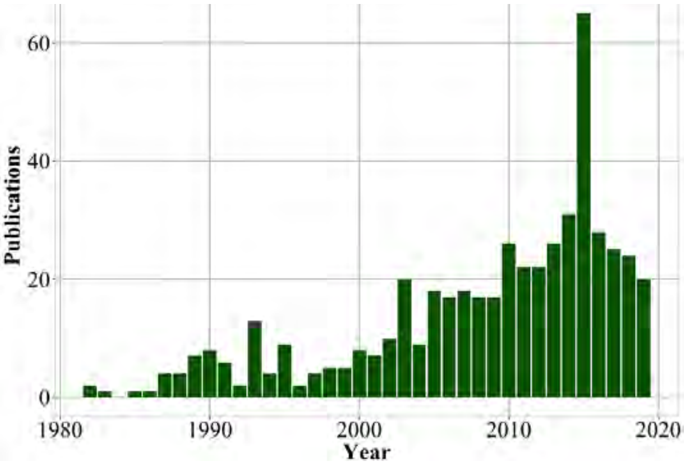

Figure 3. Publications by year utilizing specimens or data from the Mammalian Diversity of Bolivia survey.

The suite of publications spanned most aspects of mammalian biology. As would be expected with specimen-based research, the majority of papers focused on mammalian systematics, taxonomy, or phylogeography. Specimens used in taxon accounts for larger reference works (*e. g.,* Mammals of South America, Vol 2: Rodents (Patton *et al.* 2015) were the second largest area of use. New records, distributional extensions, and taxonomic lists and keys combined to made up about 10 % of the papers. Conservation oriented papers constituted about 4 % of the total, although many of the systematic, taxonomic and distributional papers also had a conservation emphasis. The utility of holistic specimens to bridge disciplines and contribute to integrated science is evidenced by the considerable number of papers which investigated mammalian parasite or pathogen biology (Figure 4). The integration and inclusion of both mammalogists and parasitologists on all MDB expeditions resulted in likely the largest collection of mammalian endoparasites from a Latin American fauna. To this day, these archived specimens continue to be a source of novel parasite discovery.

The Google Scholar profile generated for the > 500 publications of the MDB survey (https://scholar.google.com/citations?user=860kCvYAAAAJ&hl=en&authuser=2) consists of over 20,000 citations (Figure 5a). The associated citation profile (total citations was 20,619, H-index = 68, i-10 index = 340; Figure 5b) undoubtedly has missed publications based on the MDB specimens, nonetheless, the profile demonstrates the enduring and increasing value of specimen-based holistic sampling of biodiversity (Cook *et al.* 2016; Schindel and Cook 2018), as recently summarized in the extended specimen concept (Lendemer *et al.* 2019). Far from being static specimens sitting idle in museum drawers or tissue samples slowly degrading in biorepositories

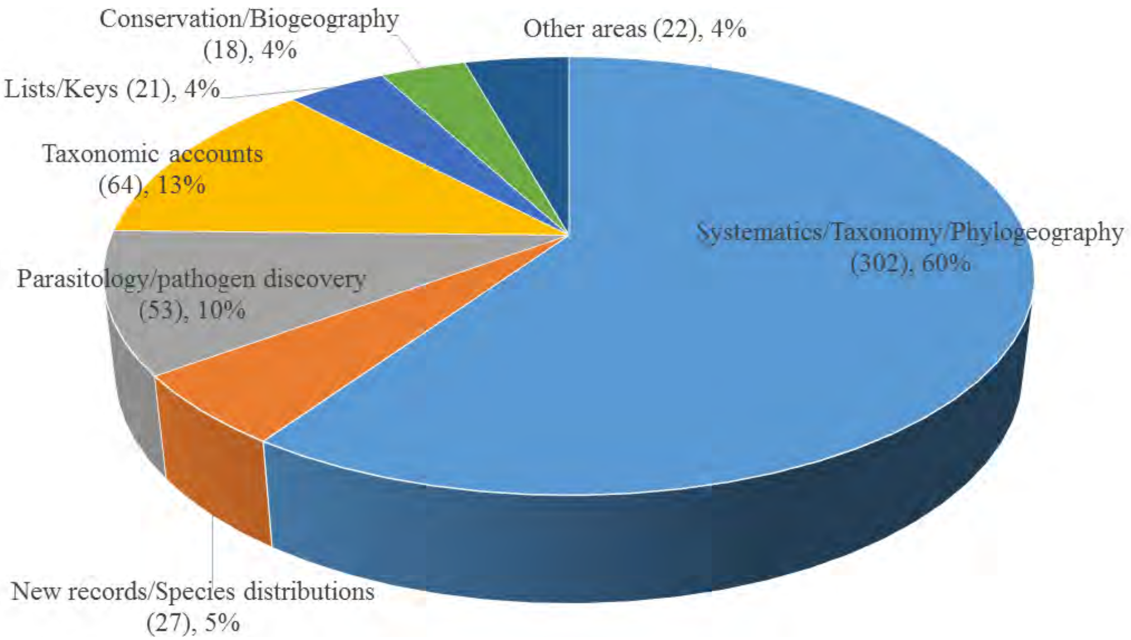

Figure 4. Breakdown of research are as of publications utilizing MDB specimens or data.

tory freezers, these materials provide a vital foundation for ever more diverse sets of investigations because our ability to probe these materials has increased due to technological advances (*e. g.,* genomics, viromics, stable isotope chemistry, 3-D ctScans, etc.) that are generating an ever-increasing body of knowledge on South American mammals and their parasites. In addition, the steady increase in citations of these publications over the past three decades demonstrates both their centrality and enduring value as these irreplaceable materials are utilized for new questions and probed with new technologies (Figure 5b).

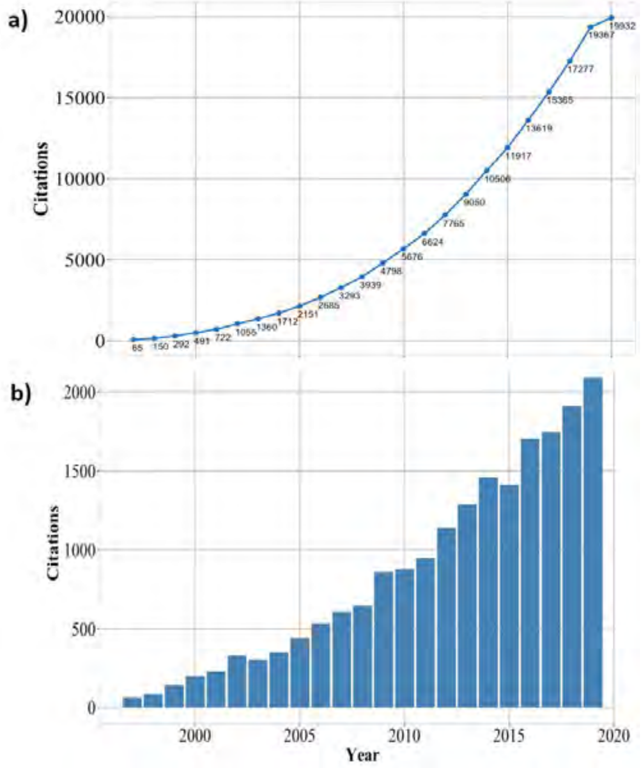

Figure 5. a) Cumulative growth curve of citations generated by MBD survey publications. b) Citations by year from the MDB survey.

A further demonstration of the power of specimens to integrate across diverse areas of investigation in biology and extend science is a MSB specimen of *Andalgalomys pearsoni* (MSB:Mamm:55245) collected from Santa Cruz department in 1984 by Sydney Anderson, Dwight Moore, and Joseph Cook in the first year of this project. That specimen was subsequently designated as the holotype of *A. p. dorbignyi* by Olds *et al.* (1987). The initial two genetic sequences were generated and accessioned in GenBank for inclusion in phylogenetic analyses accompanying the description of the new genus *Tapecomys* Anderson and Yates (2000) and a subsequent loan of material in 2002 to Scott Steppan's lab at Florida State University provided the other five sequences available in GenBank. These seven sequences have now been heavily utilized by other researchers.

Sequences in GenBank that are tied to permanent museum specimen are considered a best practice (Federhen *et al.* 2009) because these sequences can be verified and extended (from a single locus to full genomes) as technology improves our ability to probe samples. A significant percentage of GenBank data (up to 25%) are incorrectly assigned to the wrong taxon (Longo *et al.* 2011) and cannot be re-examined as they are not tied to a permanent voucher. Direct links between GenBank and museum specimens have had major consequences for research in molecular genetics, genomics, and viromics by significantly expanding the accessibility of museum resources to a wider array of the scientific community. More than 50% of requests for tissue loans made to the Division of Genomic Resources at the Museum of Southwestern Biology now originate from investigators who have discovered this resource through GenBank. GenBank accessions in turn substantially solidify the role of specimens as primary infrastructure in biology. For example, data from specimens representing rare species are often used repeatedly as our knowledge of particular groups of organisms expands. A single specimen may voucher and integrate across many independent scientific studies. The impact of each specimen thus is amplified over time as the number of associated studies multiplies (Dunnum and Cook 2012). Thus since its deposition, this specimen of *Andalgalomys pearsoni* (MSB:Mamm:55245) has been part of the foundation of 32 publications (Figure 6).

Anderson (1985) reported 277 species for the country as of 1984. The most recent treatment of mammals of Bolivia includes 406 native species (Aguirre *et al.* 2019). This is an increase of 129 species since the initiation of the MDB survey. The large increase in the number of species registered for the country since 1984 (Figure 7) corresponds to a significant increase in specimen coverage, the breadth and quality of preserved material (including "holistic specimens" with ultra-frozen tissue), digital availability via the www, a cohort of young Latin American biologists, and new approaches in systematic research that provide more detailed views of geographic variation and species limits.

In addition to new distributional records from throughout the country, many descriptions of taxa new to science are based on the MDB collections, including nine mammals (Table 2) and at least 34 parasite taxa (Table 3).

Table 2. New descriptions of mammals from the Mammalian Diversity in Bolivia survey.

Species	Citation
Andalgalomys pearsoni dorbignyi	Olds, Anderson, and Yates, 1987
Tapecomys primus	Anderson and Yates, 2000
Thomasomys andersoni	Salazar-Bravo and Yates, 2007
Ctenomys andersoni	Gardner, Salazar-Bravo, and Cook, 2014
Ctenomys erikacuellarae	Gardner, Salazar-Bravo, and Cook, 2014
Ctenomys lessai	Gardner, Salazar-Bravo, and Cook, 2014
Ctenomys yatesi	Gardner, Salazar-Bravo, and Cook, 2014
Akodon siberiae	Myers and Patton 1989
Monodelphis sanctaerosae	Voss, Pine, and Solari 2012

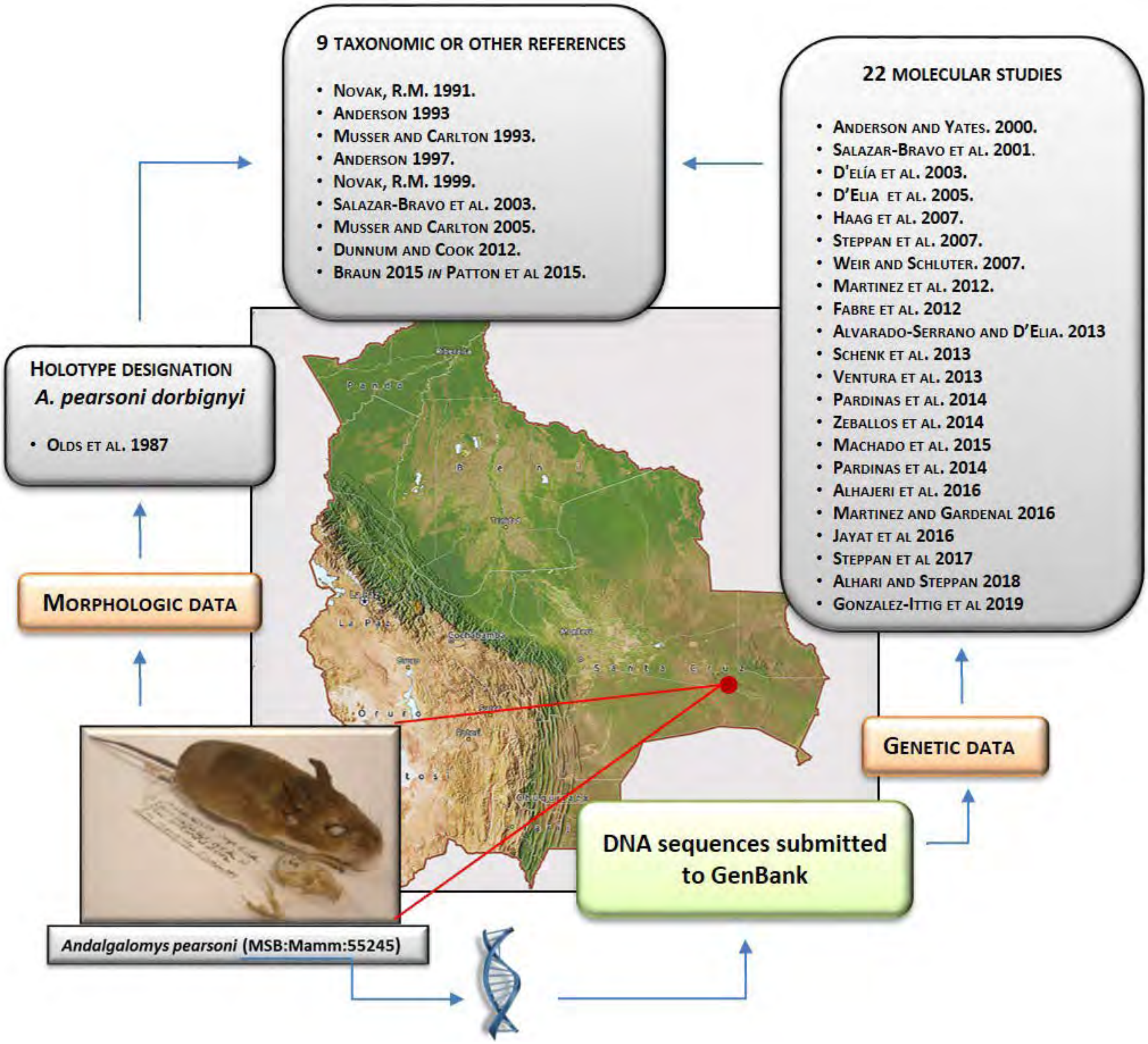

Figure 6. Citations for publications utilizing individual specimen of *Andalgalomys pearsoni* (MSB:Mamm:55245).

Type material, including symbiotype specimens (Frey *et al.* 1992) for these new taxa are held at the MSB and AMNH. In addition to the biodiversity infrastructure developed by the MDB survey, it also had a profound effect on the individuals who took part in it. The inclusion of Bolivian and American students in all aspects of the MDB surveys provided experience, inspiration, and opportunities which would have life-long implications in their scientific development.

Many of these students credit their career choices and subsequent success to experiences gained and relationships made during these expeditions. Over the course of these projects at least 75 students (13 grad students, > 50 Bolivian and 11 U.S. undergraduates) participated in field studies (Figures 8a, b) ranging from the Chaco of Tarija north to the Amazonian forests of the Pando, and from > 5000 m in the western Cordillera above the Altiplano eastward to < 500 m in the Chiquitano forests of eastern Santa Cruz. At least 29 of the students later received advanced degrees and many have now built successful careers in academia, natural history museums, or with conservation nongovernmental organizations (NGOs). The MDB survey, as well as concurrent and later USNM projects led by Louise Emmons, helped facilitate a surge in mammalogy in Bolivia and leading to a cohort of Bolivian biologists who took the torch and have now contributed massively to the understanding of the country's fauna.

Table 3. New descriptions of endo and ectoparasites from the Mammalian Diversity in Bolivia survey.

Parasite	Host Species	Citation
Andrya boliviensis	*Phyllotis osilae*	Havercost and Gardner 2010a
Andrya vesicula	*Phyllotis xanthopygus*	Havercost and Gardner 2010a
Caroloxyuris boliviensis	*Oxymycterus paramensis*	Jimenez-Ruiz and Gardner 2003a
Cryptocotyle thapari	*Lutra longicaudis*	Gardner and Thew 2006
Didelphoxyuris thylamisis	*Thylamys venustus*	Gardner and Hugot 1995
Dipetalonema yatesi	*Ateles chamek*	Notarnicola *et al.* 2007
Eimeria boliviensis	*Hydrochoerus hydrochaeris*	Casas *et al.* 1995
Eimeria cochabambensis	*Marmosops noctivagus*	Heckscher *et al.* 1999
Eimeria granifera	*Ctenomys opimus*	Lambert *et al.* 1988
Eimeria ichiloensis	*Hydrochoerus hydrochaeris*	Casas *et al.* 1995
Eimeria magnirostrumi	*Uroderma magnirostrum*	Duszynski *et al.* 1999
Eimeria marmosopos	*Marmosops ocellatus*	Heckscher *et al.* 1999
Eimeria micouri	*Micoureus constantiae*	Heckscher *et al.* 1999
Eimeria montuosi	*Ctenomys opimus*	Lambert *et al.* 1988
Eimeria opimi	*Ctenomys opimus*	Lambert *et al.* 1988
Eimeria oruroensis	*Ctenomys opimus*	Lambert *et al.* 1988
Eimeria trinidadensis	*Hydrochoerus hydrochaeris*	Casas *et al.* 1995
Helminthoxys abrocomae	*Abrocoma cinerea*	Hugot and Gardner 2000
Laelaps neacomydis	*Neacomys spinosus*	Gettinger and Gardner 2005
Lauroia bolivari	*Dasypus novemcinctus*	Jimenez-Ruiz and Gardner 2003b
Lentiella lamothei	*Proechimys simonsi*	Haverkost and Gardner 2008
Linstowia schmidti	*Thylamys venustus*	Gardner and Campbell 1992
Litomosoides andersoni	*Ctenomys opimus*	Brant and Gardner 1997
Litomosoides ctenomyo	*Ctenomys opimus*	Brant and Gardner 1997
Molinema boliviensis	*Holochilus brasiliensis*	Notarnicola *et al.* 2012
Monoecocestus andersoni	*Graomys domorum*	Haverkost and Gardner 2010b
Monoecocestus eljefe	*Galea leucoblephara*	Haverkost and Gardner 2010b
Monoecocestus microcephalus	*Graomys domorum*	Haverkost and Gardner 2010b
Monoecocestus petiso	*Galea musteloides*	Haverkost and Gardner 2010b
Monoecocestus poralus	*Phyllotis caprinus*	Haverkost and Gardner 2010b
Monoecocestus sininterus	*Tapecomys wolffsohni*	Haverkost and Gardner 2010b
Monoecocestus threlkeldi (redescription)	*Holochilus brasiliensis*	Haverkost and Gardner 2009
Pritchardia boliviensis	*Marmosops noctivagus, Marmosops ocellatus, Metachirus nudicaudatus*	Gardner *et al.* 2013
Yungasicola travassosi	*Akodon mimus*	Gardner and Perez-Ponce de Leon 2002

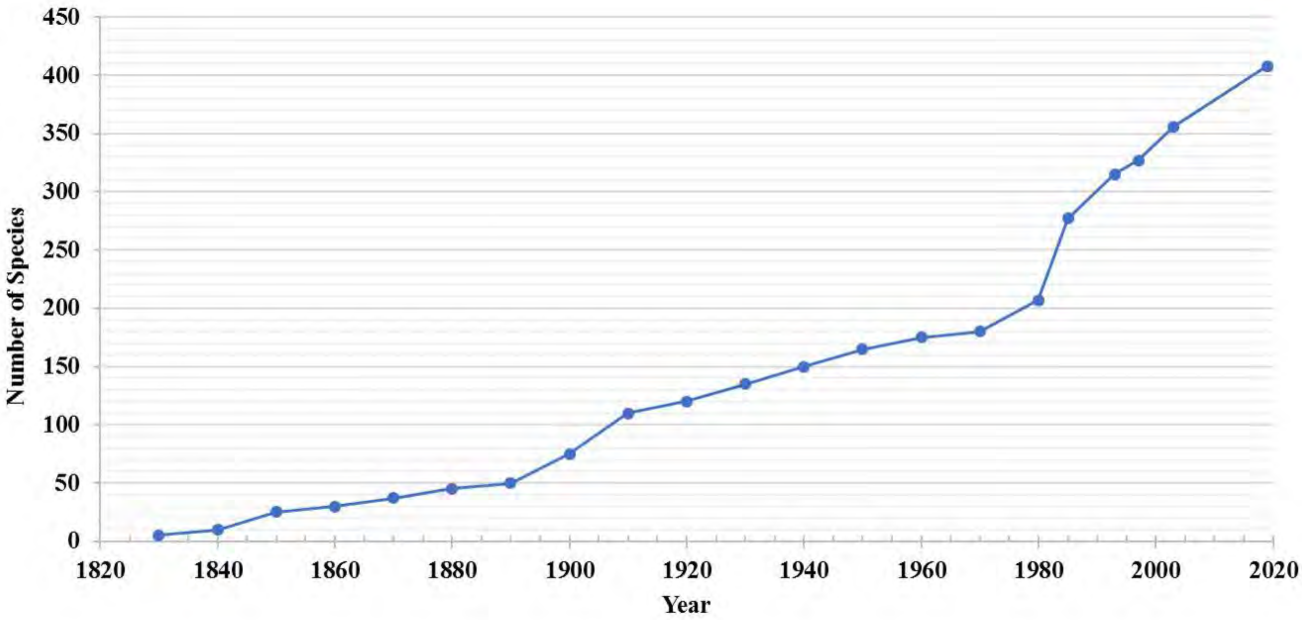

Figure 7. Accumulation of new species recorded for the country of Bolivia (modified from figure 1 in Aguirre, Tarifa *et al.* 2019).

Sydney Anderson was accorded the title of "El Padre de la Mastozoología Boliviana Contemporánea" (Tarifa 2014) for his four decades of research on Bolivian mammals and collection infrastructure. Four Bolivian mammals (*Oryzomys andersoni* Brooks *et al.* 2004; *Thomasomys andersoni* Salazar-Bravo and Yates 2007; *Oecomys sydandersoni* Carleton *et al.* 2009; *Ctenomys andersoni* Gardner *et al.* 2014) and one parasite (*Litomosoides andersoni* Brant and Gardner 1997) have now been named after Sydney Anderson. His name will certainly always be tied to the mammals of Bolivia but also to the generations of mammalogists he helped inspire and mentor along the way.

Critically, museums now not only provide materials for biodiversity studies, but they also serve a primary informatics role providing the associated original collection data (i. e., locality, date, taxonomic identity, measurements) through on-line databases (*e. g.*, Arctos), and also serve as the nexus for connecting the ever-growing sets of bigdata (*e. g.*, accessions to GenBank, IsoBank, MorphoBank, etc.) that were derived from these carefully preserved materials (Hedrick *et al.* 2020). We can confidently predict that the value and use of the Bolivian mammal specimens that were archived in multiple institutions in Bolivia and the United States under Sydney Anderson's leadership will continue to increase in the future as societal concerns related to environmental change (*e. g.*, biological annihilation, climate change, emerging zoonotic pathogens) become more pressing, scientific questions evolve, and technology continues to develop. To this point, the current COVID-19 pandemic has highlighted our general unpreparedness to respond to emerging pathogens, fundamental ignorance of our planet's natural ecosystems, and the effects of our encroachment on them. Holistic collections are ideally positioned to play a fundamental role in a proactive response to future emerging disease scenarios (Cook *et al.* 2020), a role they can only play if grown in a manner championed by Sydney Anderson and colleagues.

Figure 9. a) Mammalian Diversity in Bolivia survey students processing holistic voucher specimens (1991). From left; Mariel Campbell, Leonardo Maffei Fagale, Erika Cuellar Soto, Jon Dunnum, Forrest Davis, Jorge Salazar-Bravo, Marcello Zalles. b) Part of MDB field crew. From left: Nella Sanchez Cook, Jose Carlos Herrera, Jim Woods, Marcello Zalles, Mariel Campbell, Jon Dunnum, Forest Davis, Joe Cook) in Serrania Siberia in 1991.

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The experiences on the MDB survey were life changing and foundational to the development of our careers. Many of the relationships we made during those momentous field expeditions remain strong today and we often fondly recount our shared memories of adventures in the field with Syd. Special thanks to Jorge Salazar-Bravo, Scott Gardner and the many Bolivian and United States students who participated in the fieldwork during this decade and for their friendship, essential contributions, and in many cases, continued investment in the growth of Bolivian mammalogy and parasitology. The MDB survey collecting efforts were supported through funding from the National Science Foundation (BSR-83-16740, BSR-84-08923 Mammalian Diversity in Bolivia, BSR-86-12329, BSR-89-20617, BSR-90-15454 Mammalian Diversity in Bolivia: The Yungas and Valles (Renewal), BSR-90-24816 Parasites of Mammals of Bolivia: Phylogeny and Coevolution, INT-92-12839, and other funding agencies including the American Society of Mammalogists, Sigma Xi, The Hayward Fund at UNM, The Tinker Foundation, The Mellon Foundation (via the Latin American Institute of the University of New Mexico), The Embajada del Pais Baja in La Paz (Dutch Embassy), and Biological Society of New Mexico.

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Predation of livestock by puma (*Puma concolor*) and culpeo fox (*Lycalopex culpaeus*): numeric and economic perspectives

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Predation on livestock by wild carnivores represent large economic losses worldwide. Livestock predation by puma (*Puma concolor*) and culpeo fox (*Lycalopex culpaeus*) represents not only a problem for the Sajama National Park (SNP) management in Bolivian highlands, but also for the conservation efforts of these predators. At SNP we quantified: 1) The frequency of attacks by puma and culpeo fox on domestic livestock. 2) The effect of socio-ecological variables on the predation of livestock by these predators. 3) Estimated the losses of livestock due to other causes and compared these with the losses resulting from predation. We expected that the probability of a carnivore attack on a ranch would increase with higher livestock densities, lower abundance of wild prey, good habitat characteristics for carnivores, and low rates of husbandry and would decrease in smaller ranches and/or in areas near human settlements. We monitored predation and other causes of livestock mortality in 33 ranches for one year and estimated biomass of livestock and wild prey and monetary losses. Predators killed 183 livestock (2.3 ± 0.9 % of the animals/ranch) equivalent to $ 4,215 USD and averaging 21.8 ± 19.6 % of a family's annual income. Another 354 domestic animals died of causes unrelated to predation (201 adults and 153 yearlings), averaging 4.3 ± 4.5 % of livestock holdings per ranch. The probability of puma attacks increased with ranch size, livestock biomass and distance to the nearest town but decreased with husbandry during the dry season, while their frequency increased with ranch area. The probability of fox attacks decreased with Bofedal area, livestock biomass and better husbandry during the dry season, whereas their frequency increased when wildlife biomass decreased. Although the losses due to predation were low, the impact on the herders' economy was important. Stock mortality resulting from malnutrition, diseases, and accidents was twice as high as through predation. To reduce losses due to livestock predation and diseases, we advocate managing livestock by reducing group numbers, providing better veterinary assistance, increasing surveillance of herds during grazing events –especially during the rainy season– and through an adequate management of young animals in corrals.

La depredación del ganado por carnívoros silvestres representa grandes pérdidas económicas a nivel global. La depredación por *Puma concolor* y *Lycalopex culpaeus* es un problema para el manejo del Parque Nacional Sajama (PNS) en tierras altas bolivianas y para la conservación de estos depredadores. En el PNS cuantificamos: 1) los ataques de carnívoros sobre el ganado. 2) el efecto de variables socio-ecológicas sobre la probabilidad de ataques. 3) las pérdidas de ganado por otras causas y las comparamos con las de la depredación. Predijimos un aumento de ataques de carnívoros en ranchos con mayores densidades de ganado, menor abundancia de presas silvestres, de hábitat adecuado para carnívoros, bajas tasas de cuidado y menos ataques en ranchos más pequeños y/o en áreas cercanas a asentamientos humanos. Monitoreamos tanto la depredación como otras causas de mortalidad del ganado en 33 ranchos durante un año, como la biomasa del ganado y de las presas silvestres. Documentamos 183 animales muertos por depredadores (2.3 ± 0.9 % de los animales/rancho) equivalente a una pérdida de $ 4,215 USD para los ganaderos y de 21.8 ± 19.6 % del ingreso anual familiar. Otros 354 animales domésticos (201 adultos y 153 juveniles) murieron por otras causas, equivalente a un 4.3 ± 4.5 % del ganado por rancho. La probabilidad de ataques por puma aumentó con el tamaño del rancho y la biomasa del ganado, pero disminuyó con el cuidado y la distancia a un poblado durante la estación seca y la frecuencia de esos ataques aumentó con el área del rancho. La probabilidad de un ataque por zorro disminuyó con mayor superficie de Bofedal, mayor biomasa y cuidado del ganado durante la estación seca y los ataques fueron más frecuentes con menor biomasa de fauna silvestre. Las pérdidas por depredación fueron bajas, pero con importante impacto en la economía local. La mortalidad por desnutrición, enfermedades y accidentes fue aproximadamente el doble que por depredación. Para reducir las pérdidas por depredación y por enfermedades del ganado, debe reducirse la carga ganadera, mejorar la asistencia veterinaria, aumentar la vigilancia del rebaño –especialmente en la época húmeda– y proteger animales jóvenes en corrales.

Keywords: Andes; Bolivia; canids; carnivore conservation; felids; human-wildlife conflicts; livestock; Sajama National Park.

Introduction

The conflict derived from livestock predation by carnivores has received much attention because human retaliation has become one of the main threats for carnivore conservation around the world (Treves and Karanth 2003; Inskip and Zimmermann 2009; Treves and Bruskotter 2014; Khorozyan *et al.* 2015; van Eeden *et al.* 2017). Several approaches have been proposed, and various recommendations discussed to reduce the impacts of carnivores (*i. e.*, Graham *et al.* 2005; Treves *et al.* 2006; Kissling *et al.* 2009; Pacheco *et al.* 2008; Packer *et al.* 2009; Hoogesteijn and Hoogesteijn 2011; Zarco-González *et al.* 2012; Miller 2015). The main global lesson appears to be that, an in-depth assessment of the particularities of the conflict at the local level may be the most promising tool as the basis for an adequate mitigation strategy of any wildlife-human conflict (Zapata *et al.* 2012; Redpath *et al.* 2013).

Here, we report on an analysis of the socio-ecological variables associated to predation by pumas (*Puma concolor*), and culpeo foxes (*Lycalopex culpaeus*) on livestock within Sajama National Park (SNP), a protected area located in the Altiplano of Bolivia. The first assessment of the conflict between carnivores and livestock at SNP carried out in 1998 estimated an annual loss of 79 llamas (*Lama glama*) and 117 alpacas (*Lama* (*Vicugna*) *pacos*; Ribera-Arismendi 1999). Another research in the same area estimated that the number of llamas and alpacas, as a fraction of the total number of large animals required to maintain a puma population of ~10 individuals at SNP, coincided very closely to the numbers reported by local ranchers in terms of kills by pumas (Pacheco *et al.* 2004; Gallardo *et al.* 2009). SNP is the only protected area in the center of the Bolivian Altiplano that harbors a population of pumas, which is probably connected only to a population in the Chilean Lauca National Park, and a few surrounding areas in Bolivia with low human population density. The main areas where predation occurs at SNP have been mapped along with local herders (Ribera-Arismendi 1999), and apparently, predation was not the major cause of livestock mortality there (Zacari and Pacheco 2005). Therefore, a research assessment of the environmental and livestock management factors associated with the risk of predation is imperative to develop science-based management strategies that balance carnivore conservation with conflict mitigation (Zacari and Pacheco 2005; Weber and Rabinowitz 1996; Kolowski and Holekamp 2006; Baker *et al.* 2008; Castaño-Uribe *et al.* 2016).

A number of socio-ecological variables affect the probability of a carnivore attacking livestock. For example, predation has been shown to increase with livestock density, reductions of native prey, previous attacks in the same area, and distance from human settlements, whereas it tends to decrease closer to roads, and other areas with higher human activity (Newmark *et al.* 1994; Linnell *et al.* 2001; Conover 2002; Mazzolli *et al.* 2002; Novaro *et al.* 2004; Woodrofe *et al.* 2005; Holmern *et al.* 2007; Karlsson and Johansson 2010; Khorozyan *et al.* 2015; Ohrens *et al.* 2015). Thus, habitat characteristics are important predictors for predation risk, which in turn depends on the specific predator (Stahl *et al.* 2001; Soto-Shoender and Giuliano 2011; Abade *et al.* 2014; Zanin *et al.* 2015). In particular, for culpeo foxes, livestock predation is significantly affected by both, livestock and native prey densities (Pia *et al.* 2003). In contrast, for livestock predation by pumas the type of habitat, prey densities (both, native and livestock), and livestock management practices are important factors (Polisar *et al.* 2003).

Most human communities across the Bolivian Altiplano, including the SNP, have commonly managed the livestock predation conflict by simply killing carnivores. As a consequence, several populations have been eradicated, or severely depleted, including carrion eaters such as the Andean condor (*Vultur gryphus*), with marked ecological consequences at the community and ecosystem levels, as reported by similar functional losses in other study sites (Mech 1998; Johnson *et al.* 2001; Blejwas *et al.* 2002; Treves *et al.* 2002; Athreya *et al.* 2004). Although Gallardo *et al.* (2009) estimated that puma population at SNP was around 10 individuals (~1 puma/100 km^2), retaliation hunting due to livestock depredation was common in the area (GG, JEJ, *pers. obs.*). There is no local abundance estimate for culpeo foxes, but we infer that their numbers may be lower than in other regions of their distribution, given the high probability of retaliation hunting by locals and the large home range size (35.9 km^2) of a radio-tracked female for ~1 year at SNP (Olarte *et al.* 2009). This was the second largest estimate for this species, only below the 896 km^2 home range reported by Jiménez *et al.* (2001) and much larger than the 13.9 km^2 maximum home range size reported for females in Fray Jorge Reserve (Salvatori *et al.* 1999), both in northern Chile. Therefore, SNP is under a scenario of intense conflict between carnivores and livestock, which is worrisome giving that this protected area harbors protected populations of two of the largest carnivores occurring in the highlands of South America. Consequently, a much-needed contribution to managing the problem entails an analysis of environmental factors that may influence livestock attack. Specifically, in this study we assessed the relative contribution of socio-ecological variables influencing the probability of an attack at the ranch level within SNP. We predicted that the probability of a carnivore attack on a ranch would increase with a) higher livestock densities, b) lower abundance of wild prey, c) good habitat characteristics for carnivores, such as dense vegetation cover, and a rocky structure, and d) low vigilance by ranchers and their watchdogs. Likewise, we predicted that fewer attacks would be associated with e) smaller ranch areas and f) livestock foraging in areas closer to the nearest human settlement. To examine the relative importance of livestock deaths caused directly by carnivores, we also considered new information on other non-predation related factors affecting livestock mortality at the SNP.

Materials and methods

Study area. The Sajama National Park is located on the western portion of the Bolivian Altiplano (-17° 55´ to -18° 15´ S, -68° 41' to -69° 10' W), encompassing 100,230 ha at elevations ranging from 4,200 to 6,540 masl. It receives about 400 mm of annual rain, mainly between November and April. Mean annual temperature is 3.4 °C, with a maximum mean of 17.2 °C and a minimum mean of -12.9 °C, during the wet and dry season, respectively. The region is part of the Southern- and the Desert Puna ecoregions of Bolivia (Ibisch *et al.* 2003), where three vegetation types are distinguished: 1) Keñual-Roquedal, a rocky landscape with sparse forest cover of *Polylepis tarapacana* trees (locally known as *keñua*), which grows up to 5,200 m in elevation. Rocks are commonly covered by plants such as *Azorella compacta, Parastrephia quadrangularis* and *Poa asperiflora*. This type of habitat is found at higher elevations, where pumas and vicuñas (*Vicugna vicugna*), the main prey for pumas in terms of biomass (Pacheco *et al.* 2004), commonly find shelter; 2) Pajonal-Tholar, a steppe type of habitat with softer soil and dominated by *Festuca orthophylla*, *Stipa ichu*, and *Calamagrostis* spp., interspersed with shrubs such as *Parastrephia lepidophylla* and *Baccharis santelicis* (locally known as *tholas*); and 3) Bofedal, a lowland wetland ecosystem dominated by an hydrophilous cushion-type vegetation, dominated by *Distichia muscoides* and *Deyeuxia curvula* (Ribera-Arismendi 1999).

Human population at SNP is distributed in five local communities: Caripe, Lagunas, Manasaya, Papelpampa, and Sajama (Figure 1), with a total population of < 800 people estimated a few years before this study (Espinoza-Terán 2001). The main economic activity at SNP is livestock husbandry, mainly of camelids, which are raised in an extensive fashion, encompassing mostly Bofedales, and Pajonal-Tholar, as it is usually the case in the Bolivian Altiplano (Cardozo 1985). At the time of this study, the total livestock at SNP was composed of ~24,000 llamas, ~21,000 alpacas, and ~4,000 sheep distributed in 103 ranches and well over the carrying capacity of the environment (Espinoza-Terán 2001; local ranchers, *pers. comm.* 2006). As wild camelids, ~3.810 vicuñas roamed free at SNP (Asociación Regional de Comunidades Manejadoras de la Vicuña del Parque Nacional Sajama 2006; Gallardo *et al.* 2010).

Three of the four camelid species occurring in Bolivia (Anderson 1997) inhabit SNP. According to local people, the guanaco (*L. guanicoe*) was eliminated a few decades ago due to hunting pressures. Llamas and alpacas are reared separately, based on species and sex. Females are usually maintained near rural houses at night (but not always in enclosures), and taken to the best pastures (bofedales) during the day, usually below 4,400 masl; although they are sometimes left alone for up to a week. Sheep are usually kept along with female camelids but are confined close to houses at night. Male llamas are maintained away from females, usually in the mountain slopes closer to Keñual-Roquedal (> 4,400 masl). During mating, flocks are joined, and herders closely follow males as they tend to be aggressive toward females and may harm them during courtship. Ranchers use a seasonal movement system for livestock management. During the warm and rainy season, animals are moved to higher areas, and during the cold and dry season, they are taken back to lower elevations (~4,200 masl) to Bofedales. The vicuña, a wild camelid, is the main large prey of pumas at SNP (Pacheco *et al.* 2004). Vicuñas have been subjected to a live-shearing harvest program for about 18 years.

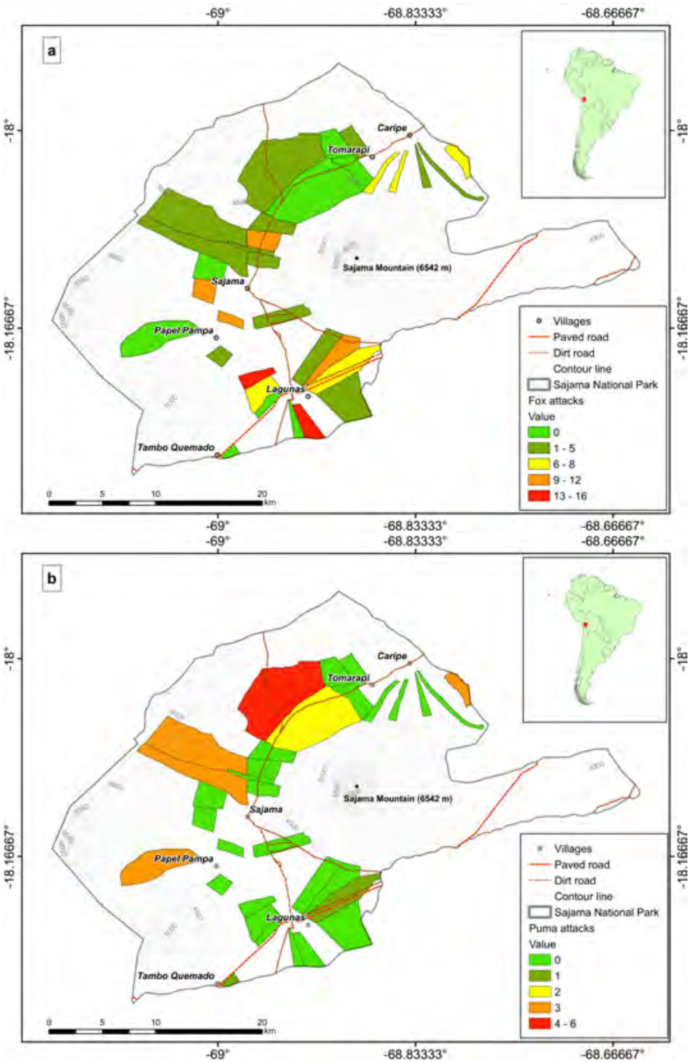

Figure 1. Study area and spatial distribution of the number of a) puma and b) culpeo fox attacks to livestock on 33 ranches in Sajama National Park, Bolivia, during 2006.

Livestock husbandry at Sajama National Park. We followed all husbandry activities from January through December 2006 within 33 randomly selected ranches (we did not distinguish between ranches with or without previous carnivore attacks). At each ranch, we interviewed one adult person (either the owner, or the responsible for livestock operations) to obtain the following husbandry information: 1) Seasonal (dry vs wet) spatial distribution of llamas, alpacas, and sheep within the ranch and according to the three vegetation types. 2) The number of people simultaneously looking out for livestock per day. 3) Effort allocated to livestock vigilance as hours/person/week/area, assessed seasonally. 4) Number of shepherd dogs per ranch. 5) Number of domestic animals killed by culpeo foxes, pumas, and other causes (poor-nutrition, diseases, and accidents) during 2006. This information was validated by field confirmation of dead animals.

Prey availability. We estimated abundance of livestock (llamas, alpacas and sheep), vicuñas, Mountain vizcachas (*Lagidium viscacia*), and small mammals. We standardized data as prey biomass per ranch (kg/area) and calculated prey availability for each ranch as follows: a) Livestock abundance and age structure based on rancher's knowledge. b) Abundance and biomass for vicuñas according to the SNP annual census carried out in August 2006 (Asociación Regional de Comunidades Manejadoras de la Vicuña del Parque Nacional Sajama 2006). Census procedures include mapping each vicuña group by experienced observers and counting the number of individuals. These locations were digitalized using a GIS to estimate an approximate number of vicuñas at each ranch. c) We estimated the biomass of Mountain vizcacha by sampling six Mountain vizcacha colonies of various sizes, in which we collected fresh feces along a 1-km long and 1-m wide transect per colony. We used the abundance of feces as an index of vizcacha relative abundance, as have been found elsewhere for Mountain vizcachas (Walker *et al.* 2000) and other Chinchillidae (J. E. Jiménez, *unpubl. data*). The biomass of Mountain vizcacha was based on abundance indices (fresh fecal pellets/area) obtained in the field and vizcacha density estimates obtained by the method of direct counts, as calibrated for the SNP by Gallardo *et al.* (2004). We projected these estimates to the area covered by the Keñual-Roquedal habitat at each ranch, which is the habitat type almost exclusively used by vizcachas at SNP. d) We estimated the density of small mammals (all species combined) at each of the three habitat types by sampling a grid of 10 x 10 Sherman traps, separated 10 m from each other and operated during five nights per habitat, only during the dry season. We baited the traps with a mixture of oats, peanuts, vanilla, and margarine. Traps were checked every morning between 7:00 and 10:30 hrs. Captured animals (only rodents) were marked with a numbered tag for subsequent identification. Abundance was estimated via capture-recapture methods (White *et al.* 1982).

Estimating probability and frequency of attacks. Several visits to ranches were carried out to confirm all predation events during 2006. For each predation event we recorded: date, prey species, age class of killed individual (young = individuals < 1 year and adults = individuals > 1 year), predator species (according to characteristics described in Shaw *et al.* 1987, the experiences of the ranchers, and of our own), exact location, type of habitat where the attack occurred, estimated value of the killed animal, and the owners name. We referred to an attack as a kill by a predator.

Data analyses and modeling. To calculate the biomass of the different animals considered in the study, we used a body mass estimate for each species to extrapolate it at the ranch level, considering the species-specific (except for rodents that were treated as a group) estimated abundances (see above). Thus, for livestock, we used the average body mass estimates provided by local ranchers: 60 kg for adult llamas, 23 kg for young llamas, 45 kg for adult alpacas, 19 kg for young alpacas, and 25 kg for all sheep. Note that these values for llamas and alpacas were very conservative, as these were below the lowest weight for the size ranges estimated for the country: 65-110 kg for llamas, and 50-70 kg for alpacas (Cardozo 1985). The low weights provided by the ranchers were likely the result of the oversized stock in the area. Following the rancher's opinion on the economic value of killed animals, we used an estimate of $ 13.0 USD for a sheep, $ 48.5 ± 16.9 USD for an adult camelid, and $ 8.6 ± 11.1 USD for a young camelid. These economic values, however, were not used in the modeling analyses. For vicuñas, we used an average body mass of 40 kg for an adult, and 10 kg for a young one (according to unpublished data from Asociación Regional de Comunidades Manejadoras de la Vicuña del Parque Nacional Sajama 2006). We used an average weight of 1.5 kg for Mountain vizcachas (Yensen and Tarifa 1993). For small mammals, according to our average field estimates, we used a density of 7.3 ind/ha, with an average 30.8 g/ind to estimate biomass for Keñual-Roquedal, and 15.5 ind/ha, with an average of 22.8 g/ind for the biomass estimate in Pajonal-Tholar. We had zero captures in the Bofedal, so this habitat type was excluded from further analysis.

We extrapolated the above estimates to the area covered by each habitat type using GIS tools. We obtained GPS locations (with the owner's supervision) and plotted each ranch on a vegetation map of SNP (Resnikowski 1997) using ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA, U.S.A.). We then calculated the area for each ranch, and the area covered by each vegetation type within that ranch. We also estimated the distance from the mid-point of a ranch to both, the closest human settlement, and the main small dirt road.

We used the data estimated above to model independently the probability and frequency of an attack on livestock by puma and culpeo fox at the ranch level. We used general linear models (GLMs) and a multimodel inference approach (Burnham and Anderson 2002, 2004) for modeling the likelihood of an attack as explained by the estimated variables, using each ranch as a replicate. Before any general linear modeling was run, however, we conducted pairwise Spearman correlations among all predictor variables to avoid collinearity in the models. All significant correlations with an $r_s > 0.9$ were considered highly correlated and we eliminated the least relevant variable. In all GLM models, we finally included eight predictor variables: a) ranch area, b) area of the Keñual-Roquedal habitat, c) adult livestock biomass, d) wildlife biomass (vicuña + Mountain vizcacha), e) small mammal biomass, f) distance to the closest human settlement, g) level of husbandry during the dry, and h) during the wet season. Separate estimates of vicuña and Mountain vizcacha biomass were highly correlated with wildlife biomass, so they were excluded from the GLM models. For both puma and culpeo fox we modeled two sets of GLMs based on the type of response variable considered. The first set estimated the probability of an attack using a GLM with binomial distribution and a Logit link function (logistic regression *sensu* Quinn and Keough 2002). The response variable considered whether a ranch was either attacked (1) or not (0). The second set of models estimated the number of attacks using a GLM with Poisson distribution and Log link function (Poisson regression *sensu* Quinn and Keough 2002). Here, the response variable was the number of attacks at the ranch level.

Given the large number of models needed to be compared, model selection was based on an autonomous selection process within a multimodel inference approach using the R package *glmulti*. This approach ranks models from best to worse based on the Akaike Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson 2002, 200). When more than one candidate model was selected (*e. g.*, ΔAIC ≤ 2) we used model averaging to estimate parameter values proportional to their Akaike weights (w_i). We also calculated a pseudo-R^2 for the candidate model with the highest number of variables to estimate the proportion of the variance explained. Finally, we compared the livestock husbandry management between seasons with a Wilcoxon test. All statistical analyses were run using SPSS 14.0 (SPSS 2005) and R 3.6.3 (R Development Core Team 2020). Descriptive results are presented as means and one standard deviation (mean ±1 SD).

Results

Characteristics of livestock husbandry. The total number of domestic animals under study was 11,490 for the 33 ranches, including a 50.2 % of llamas, 41.9 % of alpacas, and 7.9 % of sheep, representing ~24 % of the livestock and 34 % of the ranches present at SNP. Mean number of individuals per ranch was 348 ± 233, with an average density of 1.1 ± 1.5 ind/ha (range 104 to 1020 ind/ranch). Mean ranch area was 684.4 ± 744.1 ha. Most of the ranches (~70 %) harbored between 104 to 400 animals, while only 6.1 % of the ranches had more than 800 animals.

At SNP only one family member cares for grazing animals, frequently it was a child. During the dry season, people allocated a smaller amount of time to female livestock vigilance (25.3 ± 12.5 h/week) than during the rainy season (46.3 ± 21.2 h/week, $W = 785.1$, $P < 0.001$). Only 21 % of the ranchers had male livestock and this was visited once a week or every other week during the dry season and usually every other day during the rainy season. Ranchers argued that raising male livestock is usually avoided because of recurrent attacks by pumas and because they prefer to allocate more time to other economic activities, such as trading, public transportation, and tourism.

Only 22 (67 %) of the ranches raised dogs, totaling 32 dogs of which only one was a shepherd dog. All ranches had enclosures built near human settlements with a variety of materials including rocks, mud, plants, and *Polylepis* branches. Enclosures were of different sizes, but 76 % were around 8 m in diameter, and 1.6 m in high (none was higher than 2 m). Most were used mainly for vaccination campaigns during the dry season. Enclosures are not used during the rainy season, because they remain wet and increase the transmission of parasites, and diseases. Sanitary care at SNP was deficient. Only 66 % of the ranchers carried out sanitary campaigns, but those were only partial, as vaccinations were applied only to mothers and youngsters, mostly using inadequate dosages.

Livestock predation by puma and culpeo fox and its correlates. To quantify the number of attacked animals we only considered those that we were able to confirm *in situ* as killed by a carnivore (84.4 % of all the reported cases). Pumas killed 27 livestock heads, mostly adult camelids (74.1 %), particularly llamas (51.8 %). We did not record any puma attacks on sheep. Of the 156 animals killed by foxes, 90.4 % were young camelids of which 51.6 % were alpacas. Only 18 young sheep were killed by culpeo foxes during our year of monitoring. However, foxes also killed six adult (two years old) llamas and nine adult alpacas during the study (Table 1).

Most attacks by puma (81.5 %) occurred at elevations above 4,500 masl, and away (2,974 ± 3,014 masl) from human settlements; 78 % of these occurred in Keñual-Roquedal habitat type. On the contrary, 89 % of culpeo fox attacks occurred within Pajonal-Tholar, below 4,500 masl, and relatively close (98 ± 78 m) to enclosures. Ranch area was positively correlated with the area of Keñual-Roquedal ($r_s = 0.450$, d. f. = 32, $P = 0.009$), distance from human settlements ($r_s = 0.741$, d. f. = 32, $P < 0.001$), and livestock abundance ($r_s = 0.601$, d. f. = 32, $P < 0.001$).

Livestock losses due to predators. We recorded 183 domestic camelids killed by wild predators during the year of the study (1.6 % of the total heads under study); unleashed dogs killed only one young llama. Foxes were

Table 1. Distribution of livestock losses according to the cause of death, during one year at Sajama National Park, Bolivia.

	Prey type						
Mortality agent	**Adult Llama**	**Young Llama**	**Adult Alpaca**	**Young Alpaca**	**Unidentified domestic camelid**	**Young sheep**	**Total**
Puma	14	4	3	3	3*	0	27
Culpeo fox	6	39	9	70	14**	18	156
Total	20	43	5	80	17	18	183
Other causes					354		

* All adults ** All yearlings

responsible of 85.2 % of the attacks; the rest occurred by pumas. Estimated economic damage totaled ~$ 4,215 USD; ~$ 2,898 USD by foxes, ~$ 1,310 USD by pumas, and ~$ 6.7 USD by dogs. These figures represent the values for 2006 not adjusted for inflation. Predators killed an average of 2.3 ± 0.9 % of the ranches' heads, with a mean of $127.7 ± 113.2 USD of economic damage per ranch. Around 51 % of the ranches lost < $ 100 USD to predators during the year of study.

Fifty eight percent of the ranches reported predation only by foxes, 12 % only by puma, and 18 % by both predators, with 12 % reporting no losses to predators. The highest number of puma attacks (11 or 40.7 %) was recorded in ranches near the mountains to the NW of SNP, which were also the largest ranches; whereas most attacks by culpeo foxes (44.2 %) occurred in the plains to the S of SNP. Of all the attacks, 84 % occurred during the wet season (January through March; Figure 1). It is interesting to note that ranches with more puma attacks suffered less attacks by foxes and *vice versa*. An exploratory analysis showed, however, a negative yet marginally significant correlation between the number of attacks by pumas and the number of attacks by culpeo foxes at ranches ($r_s = -0.33$, $n = 33$, $P < 0.06$).

Livestock losses due to other causes. We recorded 353 dead animals that did not show signs of predation, almost two-fold of those killed by predators (Table 1). Among the attributed causes of those deaths were diseases, malnutrition, abortions, and broken limbs. Most deaths were of adult animals (201 vs 152 juveniles), which amounted an estimate of $7,545 USD. This shows that ranches under study lost more animals to other causes (10.7 ± 8.8 animals/ranch) than to both predators combined (5.5 ± 4.3; $t = -3.25$, $n = 33$, $P = 0.002$).

Probability of puma attacks. Of the 256 possible variable combinations (models), the autonomous model selection identified three candidate models (ΔAICc ≤ 2) that best explained the probability of a puma attack on ranches (Table 2). These models, in decreasing order of importance, based on averaged parameter values and Log Odd ratios, included ranch area, livestock biomass, and husbandry during the dry season (Table 2). These variables explained 44 % of the variability in the attacks by puma. As the ranch area increased, so did the probability of having a puma attack, being higher than 50 % in ranches larger than 800 ha and almost certain in those having > 1,500 ha (Figure 2 a, b). Likewise, as livestock biomass increased on a ranch, so did the probability of a puma attack, being over 50 % in ranches having ≥ 90 kg/ha of livestock (Figure 2 c, d). Although livestock husbandry during the dry season negatively affected the probability of suffering a puma attack, its effect was rather weak. There was only a 20 % probability of having a puma attack during the dry season in ranches with no husbandry (Figure 2 e, f).

Frequency of puma attacks. Six candidate models (ΔAICc ≤ 2) best explained the number of puma attacks on ranches (Table 2). These models included the density of small mammals, extent of the Keñual-Roquedal habitat, ranch area,

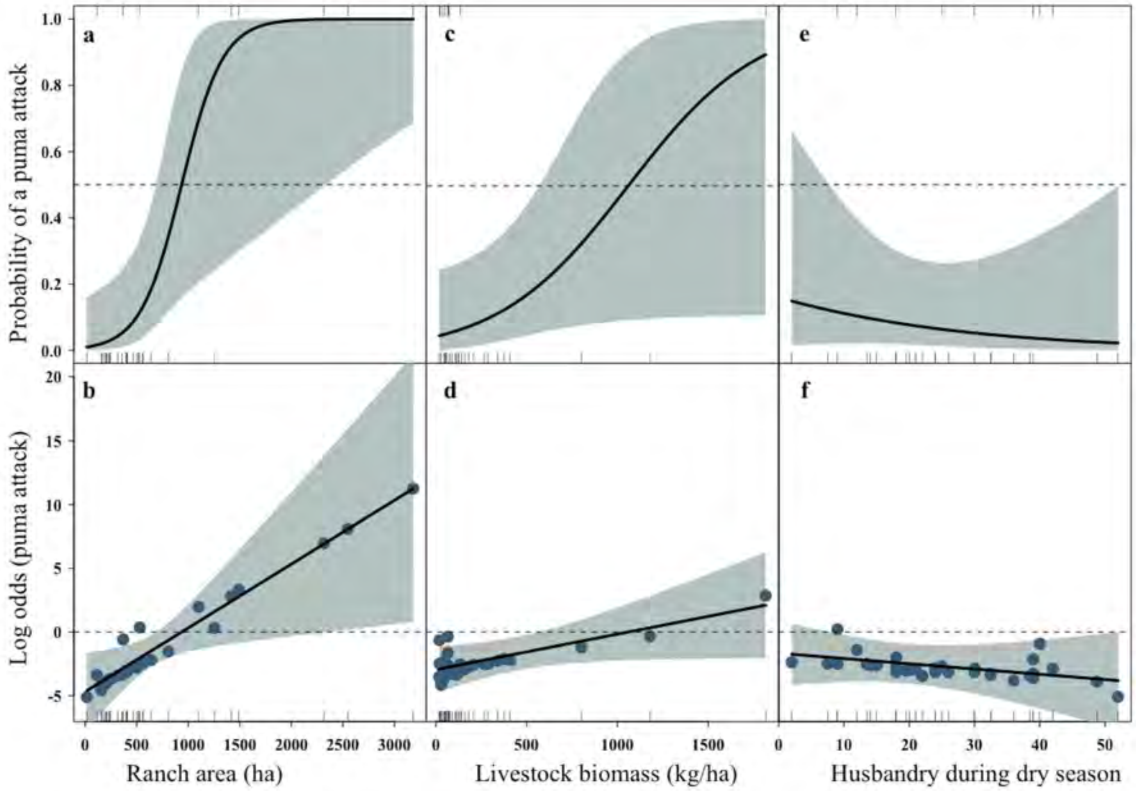

Figure 2. Changes in the probability of puma attacks in relation to socio-ecological variables at Sajama National Park, Bolivia, during 2006. Probabilities are based on odds and log odds ratios from logistic regression GLMs in combination with autonomous multimodel selection. a) Variation in the probability of an attack and b) log odds of an attack due to changes in ranch area (ha). c) Variation in the probability of an attack. d) Log odds of an attack due to changes in livestock biomass (kg/ha) across ranches. e) Variation in the probability of an attack. f) Log odds of an attack due to investment in husbandry during the dry season (h/person/week/area). Grey areas represent the 95 % CI from the model for each variable; dashed lines represent the 50/50 % chance of being attacked; dots are values at the ranch level and thin lines along the top and bottom of each graph show the distribution of values for the predictor variables.

and distance to roads as predictors. Although, these four variables explained 64 % of the variability in the frequency of puma attacks, ranch area was the most important variable (95 % CI did not include zero; Table 2). Ranch area was included in all six models. As ranch area increased, the number of puma attacks increased slightly, at a rate of one attack per every 1,000 ha of ranch increase (Figure 3 a,b). In general, the models indicated that once a puma attacked a ranch, the frequency of attacks depended very little on other socio-ecological variables.

Probability of culpeo fox attacks. Ten models (ΔAICc ≤ 2) best explained the probability of a fox attack on ranches (Table 3). These models included husbandry, both during the wet and during the dry season, livestock biomass, small mammal biomass, vicuña biomass, and the area of Bofedal habitat. Model averaging indicated that husbandry during the wet season was the most important variable, followed by husbandry during the dry season, and the area of Bofedal habitat. The other three variables had odd ratios less than one, indicating that the probability of an attack due to these variables was lower than the probability of not having an attack on a ranch (Table 3). Altogether, the six variables explained only 15 % of the variation. Usually, as husbandry increased in both seasons, the probability of an attack by foxes decreased. Attack probabilities lower than 50 % were reached when people allocated at least from 50 to 60 h/week of vigilance (Figure 4 a-d). Likewise, as Bofedal area increased on a ranch the probability of a fox attack decreased, although the probabilities remained high (> 50 %) regardless of the area (Figure 4 e, f).

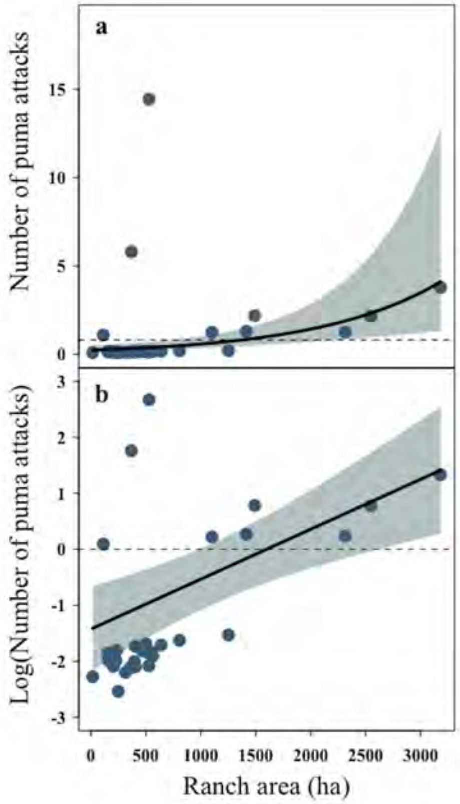

Figure 3. Changes in the frequency of puma attacks in relation to socio-ecological variables at Sajama National Park, Bolivia, during 2006. The number and log number of attacks in the model came from Poisson regression GLMs in combination with autonomous multimodel selection. a) Variation in the number of attacks and b) Log of number of attacks (linearized relation) with changes in ranch area (ha). Shaded areas represent the 95 % CI from the model for each variable; dashed lines represent the mean number of attacks and dots are values at the ranch level.

Frequency of culpeo fox attacks. Two candidate models (ΔAICc ≤ 2) that explained the number of fox attacks on ranches were selected (Table 3). These models included in decreasing order of importance, based on averaged parameter values and their 95 % CI, ranch area, vicuña biomass, livestock biomass and husbandry during the wet season. The effect of husbandry during the wet season was negligible (95 % CI of the parameter estimate included zero; Table 3).

Table 2. Autonomous multimodel selection processes on the influence of socio-ecological variables over the probability and frequency of attacks on livestock by puma at Sajama National Park during 2006. Models for the probability of attacks are based on logistic regression GLMs, whereas for the frequency of attacks are based on Poisson regression GLMs. In each case, models are ordered by their AICc values and Akaike weights (w_i) which are calculated based on the log likelihood of the model (logLik). Of all possible models (*i. e.*, 256), we show only those models with a difference in AICc (ΔAICc) ≤ 2 with the best-fitted model (lowest AICc) and their respective model average (and 95% CI) for the parameters included in the models. Parameter estimates are in terms of log Odds and Odds ratios for the probability of an attack and in terms of slopes for the frequency of an attack. An empty cell for a given variable indicates that the variable was not included in the selected model.

Dependent variable	AICc	ΔAICc	w_i	df	logLik	Dry season husbandry	Small mammal density	Ranch area	Area of Keñual-Roquedal	Distance to roads	Livestock biomass
	27.10	0	0.27	3	-10.15			0.0042			>0.0001
Probability of an attack	28.70	1.50	0.13	2	-12.13			0.0029			
	29.10	1.96	0.10	4	-9.83	-0.0413		0.0050			>0.0001
Average parameter						-0.0041		0.0041			>0.0001
Log Odds ratio						0.9595		1.0041			1.0000
Odds ratio (95 % CI)						(0.86-1.07)		(1.001-1.007)			(0.999-1.001)
	77.60	0.00	0.12	3	-35.39		-0.1609	>0.0001			
	77.70	0.09	0.11	3	-35.43			>0.0001		>0.0001	
Frequency of an attack	77.90	0.26	0.10	2	-36.73			>0.0001			
	78.30	0.69	0.08	3	-35.73			>0.0001	0.0025		
	79.10	1.45	0.06	4	-34.81		-0.1199	>0.0001		>0.0001	
	79.30	1.65	0.05	4	-34.91		-0.1342	>0.0001	0.0018		
Average parameter							-0.1445	>0.0001	0.0022	>0.0001	
Slopes (95 % CI)							(-0.35-0.07)	(>0.0001-0.001)	(-0.001-0.005)	(-0.0001-0.0003)	

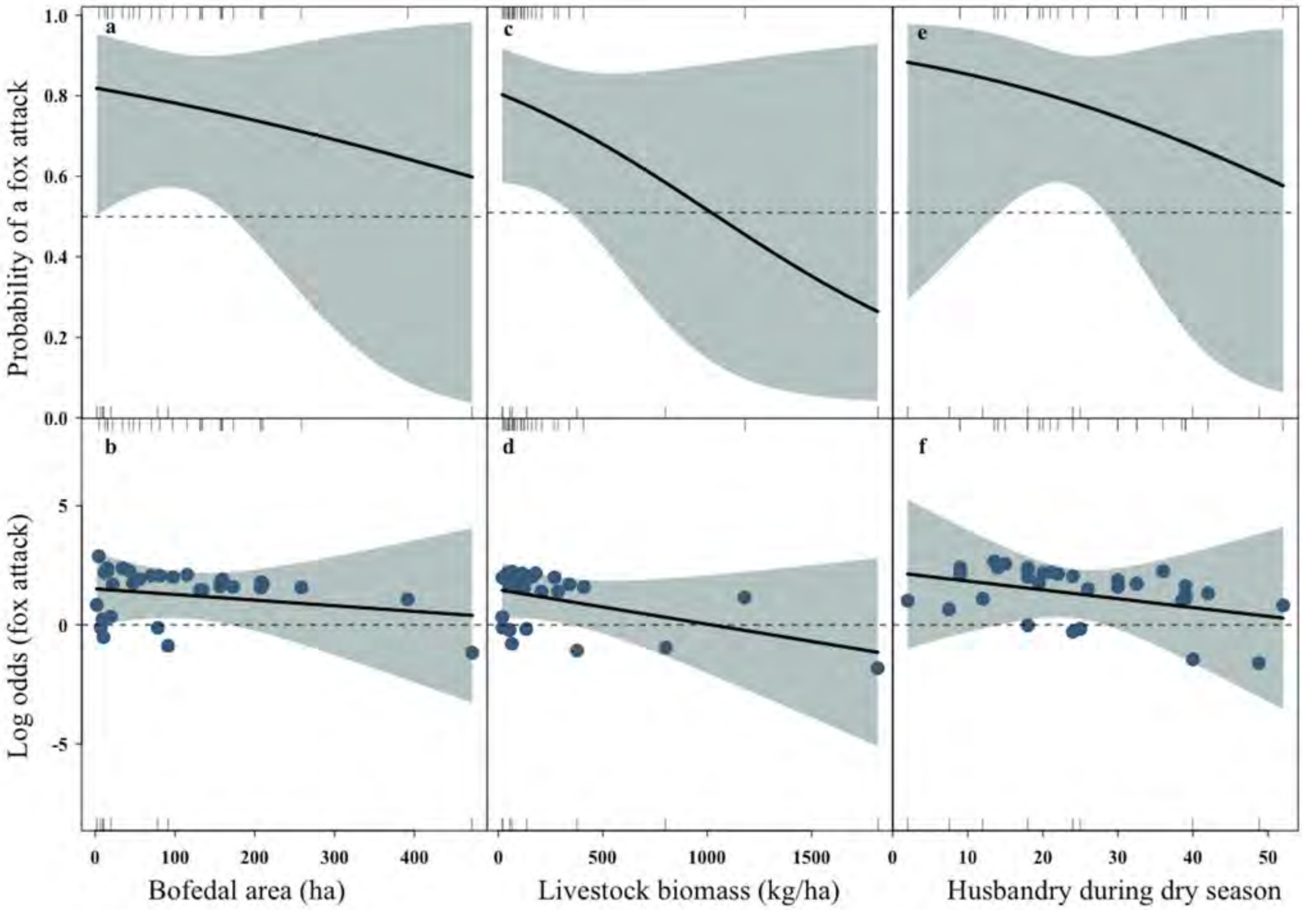

Figure 4. Changes in the probability of culpeo fox attacks in relation to socio-ecological variables at Sajama National Park, Bolivia, during 2006. Probabilities are based on odds and log odds ratios from logistic regression GLMs in combination with autonomous multimodel selection. a) Variation in the probability of an attack, and b) log odds of an attack due to changes in Bofedal area (ha). c) Variation in the probability of an attack. d) Log odds of an attack due to changes in livestock biomass (kg/ha) across ranches. e) Variation in the probability of an attack. f) Log odds of an attack due to investment in husbandry during the dry season (h/person/week/area). Shaded areas represent the 95 % CI from the model for each variable; dashed lines represent the 50/50 % chance of being attacked; dots are values at the ranch level and thin lines along the top and bottom of each graph show the distribution of values for the predictor variables.

Although, the four variables explained 61 % of the variation, their slope estimates had very low values (Figure 5 a-f; Table 3). Nevertheless, as ranch area increased, the number of fox attacks decreased slightly (Figure 5 a, b). The same pattern was found for vicuña- (Figure 5 c, d) and for livestock biomass (Figure 5 e, f). As for puma attacks, our models indicated that once foxes attacked a ranch, the frequency of attacks varied very little with other socio-ecological variables.

Discussion

Most of our predictions turned out as expected, at least for pumas. The probability of a puma attack increased with greater livestock biomass per ranch, yet this probability decreased for culpeo fox attacks. The area covered by dense vegetation and rocky structure (Keñual-Roquedal habitat type) also increased the probability of receiving puma attacks. Increased vigilance by ranchers reduced – though very slightly– the probability of an attack by both predator species. Wild prey abundance, however, affected negatively only the probability of an attack by culpeo foxes.

The importance of a management strategy for predation at SNP becomes clear when considering that the local gross family annual income ranged (at the time of the study) between $290 - 1,500 USD (FAO 2005; C. Espinoza, *pers. comm.*). This means that the average loss due to predators represented 21.8 ± 19.6 % of the annual family income. This is comparable to what happens in a similar environment in Nepal, where snow leopards (*Panthera uncia*) killed 2.6 % of sheep holdings, which represented ~25 % of the annual local income (Oli *et al.* 1994). It seems low, however, when compared to what Valderrama-Vásquez *et al.* (2016) reported as an average loss of livestock (sheep and goats) to pumas ($ 110.77 USD per unit of their analysis, that included several ranches) in the Colombian Andes. The high magnitude of the problem at SNP has been pointed out by previous studies (Ribera-Arismendi 1999; Pacheco *et al.* 2004; Zacari and Pacheco 2005). In addition, our mortality data closely resembled those obtained several years ago at SNP by Ribera-Arismendi (1999), suggesting that losses due to predation have remained stable. This strengthens our scientific-based recommendations to support the implementation of a management strategy to lessen the conflict (van Eeden *et al.* 2017) at SNP.

The contrasting effects of the attacks by puma and culpeo fox on livestock can be explained by their presumed foraging behaviors. Pumas, for example, predated mainly adult livestock away from human settlements, in

Table 3. Autonomous multimodel selection processes on the influence of socio-ecological variables over the probability and frequency of attacks on livestock by culpeo fox at Sajama National Park during 2006. Legend similar to that in Table 2.

Dependent variable	AICc	ΔAICc	w_i	df	logLik	Dry season husbandry	Small mammal density	Ranch area	Area of Keñual-Roquedal	Distance to roads	Livestock biomass
	38.5	0.00	0.11	2	-17.05	0.0343					
	38.7	0.20	0.10	1	-18.28						
	38.7	0.25	0.10	2	-17.17						>-0.0001
Probability of an attack	39.2	0.71	0.08	3	-16.18	0.0316					>-0.0001
	39.9	1.43	0.05	2	-17.76			-0.1704			
	40.0	1.56	0.05	2	-17.82				>-0.0001		
	40.1	1.65	0.05	3	-16.65	0.0328		-0.1481			
	40.3	1.77	0.05	2	-17.93		0.0286				
	40.3	1.84	0.04	3	-16.75	0.0317			>-0.0001		
	40.4	1.93	0.04	2	-18.00					0.0031	
Average parameter						0.0329	0.0286	-0.1598	>-0.0001	0.0031	>-0.0001
Log Odds ratio						1.0334	1.0290	0.8522	0.9998	1.0031	0.9999
Odds ratio (95% CI)						(0.98-1.09)	(0.96-1.01)	(0.60-1.21)	(0.99-1.0)	(0.99-1.01)	(0.99-1.0)
	217.1	0.00	0.23	4	-103.83			-0.0005	-0.0001		>-0.0001
Frequency of an attack	219.0	1.94	0.09	5	-103.40			-0.0004	-0.0001		>-0.0001
Average parameter								-0.0005	>-0.0001		>-0.0001
Slopes (95% CI)								(-0.0008--0.0001)	(-0.0002--0.00001)		(-0.0003--0.0002)

areas toward the mountains, where they usually find shelter; whereas culpeo foxes attacked close to human dwellings, targeted mainly juveniles and included sheep. A likely explanation for this difference is that culpeo foxes remain closer to people to avoid encountering pumas, which commonly prey on them (Pacheco *et al.* 2004). Note that guardian dogs were uncommon at SNP. Radiotracking studies are needed to address this issue.

Culpeo foxes also preyed on sheep (Ribera-Arismendi 1999), which are usually closer to ranch houses, whereas pumas preyed mainly on vicuñas (Pacheco *et al.* 2004), which are usually more abundant away from humans at SNP (Gallardo *et al.* 2010). In more general terms, an interesting interaction between culpeo foxes and pumas may develop when both co-occur. At least in the Bolivian Andes, where pumas are present in areas with livestock, a strong conflict develops due to predation, which is further exacerbated with livestock predation by culpeo foxes (Pacheco *et al.* 2010). The fact that pumas and culpeo foxes at SNP did not usually use the same habitats for preying upon livestock suggests that although these predators share the same landscapes, they tended to partition habitat types. We hypothesize that this is driven by intra-guild predation of pumas on foxes (de Oliveira and Pereira 2014).

Two other findings are notable from our results: i) dogs do not usually attack livestock at SNP. Dogs may be important predators for wildlife elsewhere in South America (Schüttler *et al.* 2018; Rodriguez *et al.* 2019), and they are usually blamed for attacking livestock in other regions of Bolivia (Aliaga-Rossel *et al.* 2012). Although dogs are well-known allies in reducing carnivore attacks (Gonzales *et al.* 2012; Novaro *et al.* 2017; Spencer *et al.* 2020), Sajama ranchers are not prone to raising dogs, because they are supposedly a source of parasites. Therefore, dogs at SNP are rather rare and problems with unleashed dogs are seldom reported. ii) Losses of domestic camelids due to diseases and undernourishment took at least twice as many heads as those preyed by both predators combined. This is in line with Zacari and Pacheco's (2005) findings, who, based on clinical examinations and theoretical mortality rates, estimated that diseases would kill two to six times more livestock than predators at SNP, a figure very close to what was estimated in this study. Furthermore, rural, non-technologically oriented rearing operations for domestic camelids (llamas and alpacas) may usually expect between 45 to 55 % fertility (Cardozo 1985; Quispe *et al.* 2009). Mortality at weaning in domestic camelids is quite high though (6 to 8 %) and adult annual mortality may reach up to 10 % (Cardozo 1985) and can be as high as 50 % under drought conditions (Quispe *et al.* 2009). It is notable that in a region nearby SNP (Turco, Bolivia), droughts have been reported by local people as the most important cause of death for domestic camelids, whereas pumas and culpeo foxes were second and third in importance, respectively, well above the importance of diseases (Romero-Muñoz *et al.* 2016). Under this scenario, a 1.6 % mortality due to predation at SNP does not seem to be high, at least as compared to losses due to pumas in central Argentinean rangelands (medians: 0.1 to 1.0 % of cattle holdings plus 3.3 to 10.4 for sheep; Guerisoli *et al.* 2017) or 0.94 % and 0.39 % of the sheep stock by pumas and culpeos, respectively, in Aysen, southern Chile (J. Jiménez et al. *unpublished data*).

Probability of attacks by predators. Although intense husbandry may reduce the probability of livestock suffering an attack by puma, ranch area and livestock biomass better predicted that likelihood. Large ranches harbored

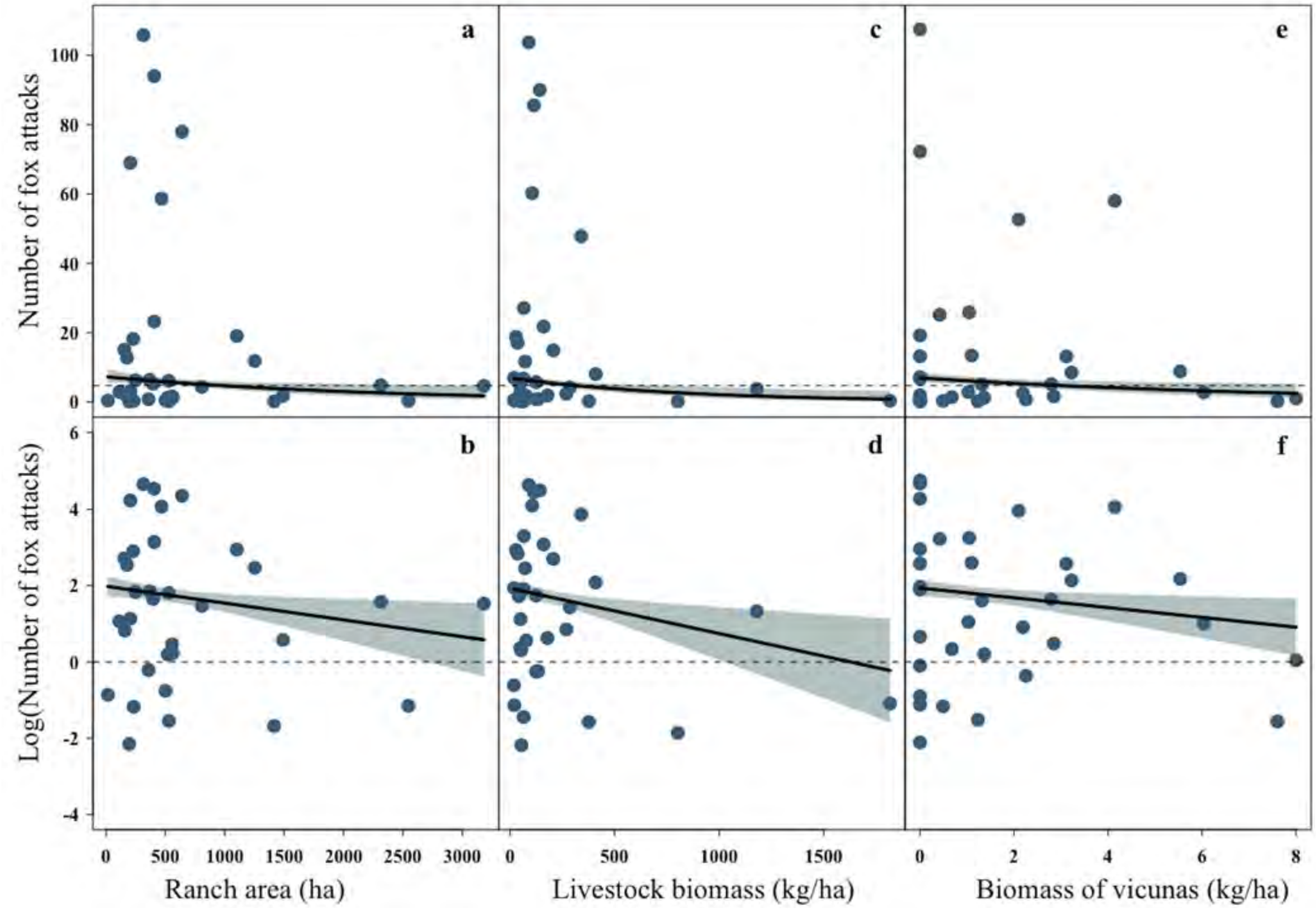

Figure 5. Changes in the frequency of culpeo fox attacks in relation to socio-ecological variables at Sajama National Park, Bolivia, during 2006. The number and log number of attacks in the model came from Poisson regression GLMs in combination with autonomous multimodel selection. a) Variation in the number of attacks and b) log of number of attacks (linearized relation) with changes in ranch area (ha). c) Variation in the number of attacks. d) Log number of attacks due to changes in livestock biomass (kg/ha) across ranches. e) Variation in the number of attacks. f) Log number of attacks due to changes in vicuña biomass (kg/ha) across ranches. Shaded areas represent the 95 % CI from the model for each variable, dashed lines represent the mean number of attacks and dots are values at the ranch level.

more livestock (number of animals), which means more potential prey, under less human supervision. Ranches > 1,500 ha in SNP have a probability close to one for receiving an attack from pumas. Furthermore, the number of livestock killed by pumas on ranches larger than 1,500 ha rises exponentially. Finally, larger ranches are usually composed of larger areas of Keñual-Roquedal habitat type, which, according to our long-time, but non-quantitative observations, as well as by locals' knowledge, is puma's preferred habitat for shelter at SNP. In other regions, predation by pumas has also been reported to be higher when livestock moves closer to forests and water, away from humans (Mazolli *et al.* 2002). The preference for pumas for rocky and vegetation cover is likely, in addition to the fact that they usually avoid areas inhabited by humans (Dellinger *et al.* 2020). Similar patterns of a positive correlation between ranch size and/or livestock numbers and predator attacks have been widely reported for a large number of predator species both in America (Mech *et al.* 2000; Treves *et al.* 2004; Bradley and Pletscher 2005; Romero-Muñoz *et al.* 2016; Sarmiento-Giraldo *et al.* 2016), as elsewhere (Kaartinen *et al.* 2009; Hanley *et al.* 2018; Mijiddorj *et al.* 2018).

Culpeo foxes seem to respond very differently than pumas to the same socio-ecological variables evaluated. The single most important variable that may be controlled through management practices is husbandry, whose rate of increase is related to a decrease in the probability of receiving an attack from culpeo foxes. Husbandry and herding have been repeatedly found to reduce predator attacks in previous studies elsewhere (Conover 2002; Treves *et al.* 2002; Treves and Karanth 2003; Ogada *et al.* 2003; Treves *et al.* 2006; Mijiddorj *et al.* 2018; Adhikari *et al.* 2020). Two other variables that were negatively related to the likelihood of fox attacks were livestock biomass and area covered by Bofedales. Although livestock uses preferentially the Bodefales to forage, it should be noted that our capture success for small mammals at the Bofedales was zero, which may partially explain the absence of culpeo foxes roaming around this type of habitat. In accordance, the study by Olarte *et al.* (2009) at SNP suggests that culpeo foxes do not select the use of Bofedales. Furthermore, Bofedales have very low vegetation cover rendering this a highly open and exposed habitat, increasing the visibility of a predator such as a culpeo fox to humans and pumas.

In a review of > 120 estimates of livestock loss to predation by carnivores across five continents, Baker *et al.* (2008) noted that it usually ranged between < 1 and 5 % of the total livestock holdings. In 6 % of the cases, however, losses by predation reached > 20 % of the stocks. Compared to other case studies, our yearly loss estimate of 1.6 % of the stock to predation was higher than the maximum of 0.59 % reported in France (Stahl *et al.* 2001) as a yearly loss of sheep due to Eurasian lynx (*Lynx lynx*) predation, but lower than the 4.6 % combined losses to jaguars (*Panthera onca*) and pumas on livestock at four sites in Costa Rica (Amit and Jacobson 2017), and even lower than the 10 % herd size losses due to Ethiopian wolves (*Canis simensis*, Eshete *et al.* 2018) or the 23.9 % losses of livestock due to wolves (*Canis lupus*) and snow leopards (*Panthera uncia*) in Mongolia (Mijiddorj *et al.* 2018). A loss of 0.25 to 5.0 % of the livestock was reported in North American and European studies, whereas it tended to be higher (< 1 to ~10 % of the total stocks) in African sites (Thirgood *et al.* 2005). Under certain circumstances, however, losses can be as high as 78 % as has been the case for goats lost to pumas in southern Brazil, after carnivores were protected (Mazzolli *et al.* 2002), or the 40 % of sheep lost to culpeo foxes in some ranches in Argentina, at times when native prey was scarce (Novaro *et al.* 2004).

The absence of a relationship between native prey biomass and probability of an attack from predators found in our study coincides with the general patterns found by Ugarte *et al.* (2019). The probability of suffering an attack by pumas and culpeo foxes reached almost 100 % for large ranches, irrespective of the wild prey biomass available. Therefore, it seems reasonable to conclude that the probability of suffering an attack at any single ranch in the SNP is quite high, but the accumulated losses to predation are rather low, as compared to other sites around the world.

Although the numerical losses at SNP may seem low, their effect on the local economy was not. Losses to predators represented between 8 to 44 % of the annual family income at SNP. Five studies from Africa and Asia reviewed by Suryawanshi *et al.* (2017) revealed that up to 50 % of the annual income may be lost to predators. Thus, our figures are not the highest. An important fact to bear in mind, however, is that the proportion of a family's income that is lost to predators, may be important when one tries to implement a mitigation measure to reduce predation (Amit and Jacobson 2017). In fact, our long-term experiences at SNP indicate that local people have very low credibility on outsiders (scientists among them) when discussing mitigation measures for wildlife depredation. This certainly adds another dimension to diminishing the conflict.

The probability of suffering an attack from pumas increased with ranch size, livestock biomass, and closeness to the rocky and well-vegetated habitats embodying shelter for pumas. Husbandry also reduced the probability of a puma attack, but only marginally. Culpeo fox attacks were more likely in ranches with less livestock biomass and a larger area covered by Bofedal. Greater attention on the herds by humans contributed to reducing the probability of a fox attack.

The most important source of mortality for domestic camelids at SNP was not predation by either pumas or foxes, but by diseases and malnutrition. This fact prompts us to pose, as a hypothesis (see Treves and Santiago-Ávila 2020), that livestock predation by carnivores at SNP may be acting as compensatory mortality, if weak animals are killed more often (*i. e.*, Bradley and Pletscher 2005). We do not have data to test this hypothesis yet.

Given that the livestock standing biomass at SNP is higher than in most of the Bolivian Altiplano (Cardozo 1985; MAPZA-GTZ 2001), increasing health care may only make things worse concerning carrying capacity (already surpassed) and, hence, overall health indices for camelids at SNP.

Although we do not have data from other regions of Bolivia to compare with, our findings on the causes of mortality at SNP let us venture to propose a few recommendations:

a) Standing livestock biomass should be reduced, to increase overall health of all domestic camelids. As an indirect consequence, fewer predation events by pumas are expected and degraded vegetation may improve.

b) Once livestock health indices have improved, the critical and feasible measure to reduce predation seems to be the increase in husbandry practices. Although our modeling shows an overall weak effect of husbandry, we must consider, for instance, that male llama groups are left alone on prime puma habitat and are only visited two to four times a month. One possibility is to establish communal herders, which should be compensated relative to the time invested in tending livestock, while providing livestock owners more free time to focus on other economic activities.

c) The use of shepherd dogs, which is highly recommended by several studies elsewhere, including Argentina (Gonzales *et al.* 2012; Novaro *et al.* 2017) should be an additional strategy to be implemented at SNP. Although local people do not like to raise dogs, their reasoning behind this attitude can be overturned if a program includes the vaccination of shepherd dogs. Clearly, an economic cost-benefit analysis of raising and caring for a shepherd dog (*i. e.*, Saitone and Bruno 2020) should be carried out before implementing such a program at SNP.

d) Other potential measures that can be implemented are the use of conditioned taste aversion and exploring a predator friendly market for camelid meat from SNP (Cowan *et al.* 2000; Aquino and Falk 2001; Pacheco *et al.* 2008). Implementing the latter would provide better revenues for herders while accepting some losses to predators.

e) Prohibit hunting of pumas as a measure to reduce attacks, given that the puma population at SNP may be too small to withstand any hunting pressure (Gallardo *et al.* 2010). If hunting for culpeo foxes is to be considered, a population assessment should be done before any actions can be taken, and learning from experience, such as the one with > 30 years of culpeo control in Argentina (Funes *et al.* 2009) should be a priority.

Acknowledgments

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Alpha-taxonomy in the cricetid rodent *Neomicroxus*, a first assessment

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Neomicroxus, a recently named genus, comprises small-bodied cricetid rodents patchily distributed in high-Andean ranges from Ecuador to Venezuela. Currently, two species of *Neomicroxus* are recognized, *N. bogotensis*, endemic to the Cordillera Oriental in Colombia and Cordillera de Mérida and Páramo de Tamá in Venezuela, and *N. latebricola* that occurs northern Andes of Ecuador. The genus is among the most poorly understood Neotropical rodents and to date no formal assessment about its alpha taxonomy was conducted. Based on DNA evidence of the first portion of the mitochondrial cytochrome b gene (cytb) and the first exon of the interphotoreceptor retinoid binding protein (IRBP), as well as craniodental measurements,we explored the divergence degree, genetic structure and phyletic relationships of the two species currently allocated under *Neomicroxus*. Our analyses support the monophyly of the genus as well as its uncertain tribal affiliation. *Neomicroxus* was retrieved as structured in two main branches, in agreement with the traditional recognition of two species. The populations referred to *N. bogotensis* exhibit deep divergence values (> 6 %) pointing to the existence of undescribed species under its concept. In contrast, populations of *N. latebricola* show a shallow genetic structure although implying recognizable geographical breaks. A moderate degree of genetic and morphological differentiation supports a new subspecies for the western populations of *N. latebricola*. Our contribution is the first attempt to better understanding the alpha taxonomy of *Neomicroxus*, highlighting the importance of the geographic complexity as a barrier to the genetic flow in *N. bogotensis* and the significance of the subspecies concept to formalize the geographic variation recovered in *N. latebricola*.

Neomicroxus, un género recientemente nominado, agrupa roedores cricétidos de pequeño tamaño distribuidos en zonas altas de los Andes, desde Ecuador hasta Venezuela. Actualmente, se reconocen dos especies, *N. bogotensis* endémica de la Cordillera Oriental de Colombia, Cordillera de Mérida y Páramo de Tamá en Venezuela, y *N. latebricola*, que ocupa el norte de los Andes en Ecuador. Este género se encuentra entre los roedores neotropicales menos conocidos y, hasta la fecha, no se ha realizado ninguna evaluación formal sobre su taxonomía alfa. Basados en secuencias de ADN de la primera porción del gen mitocondrial del citocromo b (cytb) y el primer exón de la proteína de unión del interfotoreceptor del retinoide (IRBP) e información métrica cráneo-dentaria, exploramos el grado de divergencia, estructura genética y relaciones filogenéticas de las dos especies actualmente asignadas bajo *Neomicroxus*. Nuestros análisis apoyan la monofilia del género como así también su afiliación tribal incierta. Se recuperaron dos clados principales en concordancia con las especies reconocidas dentro del género. Las poblaciones referidas a *N. bogotensis* muestran valores de divergencia profunda (> 6 %) que sugieren la existencia de una especie no descrita. En contraste, las poblaciones de *N. latebricola* muestran una estructura genética somera pero que implica quiebres geográficos reconocibles. La diferenciación genética y morfológica moderada apoyan la existencia de una nueva subespecie para las poblaciones occidentales de *N. latebricola*. Nuestra contribución es el primer intento de comprender la taxonomía alfa de *Neomicroxus*, destacando la importancia de la complejidad geográfica como barrera para el flujo genético en *N. bogotensis* y la importancia del concepto de subespecie para formalizar la variación geográfica observada en *N. latebricola*.

Keywords: Colombia; Ecuador; *Microxus; Neomicroxus bogotensis*; *Neomicroxus latebricola*.

Introduction

Among the most poorly known high-Andean cricetids is *Neomicroxus*, a genus recently erected to encompass small-bodied akodont-like sigmodontines previously placed in *Akodon* and *Microxus*. *Neomicroxus* was based on *Microxus latebricola*, originally described from a single specimen collected in Ambato, on the eastern Cordillera in Ecuador (Anthony 1924). Another species, *Acodon bogotensis*, is also included in the genus, being up to date exclusive from Colombia and Venezuela (Alvarado-Serrano and D'Elía 2013, 2015).

Paradoxically, both species of *Neomicroxus* remained taxonomically unexplored, although they are abundant and easy to catch in high-Andean environments (*e. g.*, Corporación Suna Hisca 2003; Vianchá *et al.* 2012; Brito 2013; Curay 2019; Ojala-Barbour *et al.* 2019). The deconstruction of the genus *Microxus*, after the peak of its complexity during the '30 (*i. e.*, involving *affinis*, *bogotensis*, *iheringi*, *lanosus*, *latebricola*, *mimus*, and *torques*; Gyldenstolpe 1932), was a slow and hesitant process. As late as the beginnings of the present century, the taxonomic situation of *bogotensis* and *latebricola* was summarized by Voss (2003:21) as follows "*This species [*latebricola*] closely resembles* Akodon *[sic]* bogotensis *Thomas (1895), another eastern-Andean species that was formerly referred to the genus* Microxus. *Among other shared similarities, both species differ from typical* Akodon *by their … Although phylogenetic analyses of mitochondrial DNA sequences do not support the separate generic status of* Microxus *(as represented by the type species* mimus *Thomas; see Smith and Patton [1993] and references cited therein), sequence data from* latebricola *and* bogotensis *have not been analyzed. Despite their current generic classification, these two northern-Andean endemics clearly form a distinct clade that merits nomenclatural recognition*." The advent of the first molecular data for *latebricola* was the keystone to crystallize what the acute morphological eye of Voss (2003) envisioned; *Neomicroxus* was erected with *latebricola* as type species (Alvarado-Serrano and D'Elía 2013). However, molecular findings retrieved an additional and previously unsuspected result; *N. latebricola* was neither an *Akodon* nor an Akodontini (Alvarado-Serrano and D'Elía 2013).

Almost nothing is known about the potential variability within *Neomicroxus* along the > 10º degrees of latitude which encompasses its range. Both species are found in the northern Andes at elevations above 2,400 masl and reaching as high as 3,900 masl (Alvarado-Serrano and D'Elía 2015). *N. bogotensis* is endemic to the Cordillera Oriental of Colombia and the Cordillera de Mérida and Páramo de Tamá in Venezuela, while *N. latebricola* occurs to high elevations of the eastern Andes in Ecuador, from Tungurahua to Carchi provinces (Alvarado-Serrano and D'Elía 2013, 2015). Recently, Curay (2019) revealed morphological variation within the Ecuadorian populations that supports the recognition of geographic structure in what is currently understood as *N. latebricola*. It is in agreement with the finding of populations of the species, traditionally known and restricted only to the eastern Andes, in western locations from the Cordillera Occidental such as the Páramo de Frailejones (Brito 2013). In this contribution, we undertook a reappraisal of the systematics of *Neomicroxus*, including for the first time sequences of *N. bogotensis*. We analyzed two DNA markers and morphometric variables as a first attempt to explore of the alpha-taxonomy of the genus.

Materials and Methods

Sequence acquisition. We obtained DNA sequences from specimens of *Neomicroxus* from Colombia (*n* = 3, Cundinamarca and Santander departments) and Ecuador (*n* = 2, Carchi province; Appendix 1, Appendix 2). The new molecular data consisted of five nucleotide sequences of the first portion of the mitochondrial cytochrome b gene (cytb, 801bp) and four of the first exon of the interphotoreceptor retinoid binding protein (IRBP, 1514bp). Here, we included for the first time in any phylogenetic study sequences of three specimens of *Neomicroxus bogotensis*. The monophyly of the genus, the identity of the sister group, and its phylogenetic position into the Sigmodontinae have not been fully corroborated (Alvarado-Serrano and D'Elía 2013). Therefore, we included sequences for representatives of the several tribes of Sigmodontinae and some outgroup taxa (other Cricetidae, Nesomyidae and Spalacidae) retrieved from GenBank. For those terminals that miss information, we completed the matrix with missing data or ambiguous state characters (*i.e.* N). All analyzed taxa as well as the vouchers of their cytb and IRBP sequences are listed in Appendix 2.

DNA of high molecular weight was extracted from the Ecuadorian specimens (*N. latebricola)* using the protocol of the Wizard Genomic DNA Purification kit, with fresh tissues as starting material. In the case of the Colombian specimens also DNA of high molecular weight was extracted from fresh tissues, as well as degraded DNA from ancient material (small fragments of rehydrated soft tissue adhered to cranial bones of museum specimens); a GeneJet Genomic DNA Purification Kit (Thermo Fisher Scientific) was used indistinctly for both processes. However, the ancient material was previously subjected to a repetitive washing protocol (Giarla *et al.* 2010) in order to remove foreign DNA and potential PCR inhibitors. Primer pairs used for amplification and sequencing of the mitochondrial fragment from the Ecuadorian specimens were MVZ05 and MVZ16 (Smith and Patton 1993), while for the IRBP locus we used the A1 and F1 (Jansa and Voss 2000). Amplification conditions followed Da Silva and Patton (1993) for cytb and Jansa and Voss (2000) for IRBP. For the Colombian specimens with DNA of high molecular weight (UIS-MZ 1299 and 1596), a fragment of + 800 bp of the cytb was amplified with the flanking primer L14724 (Irwin *et al.* 1991), and the internal primer O700 H (Handson and Bradley 2008), while for the specimen with degraded DNA (IAvH 5777), only + 400 base pairs of the gene were amplified with the flanking primer MVZ05, and the internal primer MVZ04 (Smith and Patton 1993). For these cytb sequences we modified the amplification conditions of Hanson and Bradley (2008). The IRBP locus only was amplified from the Colombian specimens with DNA of high molecular weight using the primers IRBP217 and IRBP1351 (Stanhope *et al.* 1992) and we followed the amplification conditions mentioned there. All reactions included negative controls. Amplicons from Ecuadorian specimens were purified and sequenced at the external service of Macrogen, Inc. (Seoul, Korea), whereas those from Colombian specimens at the Servicio de Secuenciación y Análisis Molecular SSiGMol, Universidad Nacional de Colombia (Bogotá, Colombia).

Descriptive and phylogenetic analysis. Before conducting phylogenetic analyses, we checked the quality of each DNA sequence in the edition process with CodonCode Aligner (Codon-Code 2014). Subsequently, sequences were aligned using default options in ClustalX 2.0 (Larkin *et al.* 2007). New DNA sequences were deposited in GenBank (accession numbers cytb: MT240520-MT240524, IRBP: MT249797-MT249800). Observed values of cytb sequence divergence (*p* distance) were calculated with MEGA7 (Kumar *et al.* 2016) ignoring those sites with missing data (Appendix 3). Phylogenetic analyses were conducted using the concatenated matrix and subjected to Maximum Parsimony (MP; Farris 1982), Maximum Likelihood (ML; Felsenstein 1981) and Bayesian Inference (BI; Huelsenbeck *et al.* 2001) approaches. MP analysis was carried out in PAUP* version 4.0 (Swofford 2000) with characters treated as unordered and equally weighted, 200 replicates of heuristic searches with random addition of sequences and tree bisection-reconnection (TBR) branch swapping. Nodal support was estimated by 1,000 bootstrap replicates with five replicates of sequence addition each (BT1). For the ML analysis, we used IQ-TREE version 1.6.0 software (Nguyen *et al.* 2015) implemented in the IQ-TREE webserver (Trifinopoulos *et al.* 2016) using LG+I+G4 substitution as the best-fit model. Statistical support for each individual node of the ML phylogenetic tree was estimated using 1,000 iterations of the ultrafast bootstrap value (BT2). Bayesian analyses were conducted in MrBayes 3.2 (Ronquist *et al.* 2012). We performed two independent runs, each with three heated and one cold Markov chains, were allowed to proceed for 10^7 iterations and were sampled every 1,000 generations. We used the GTR+G+I substitution model previously determined by Akaike information criterion (AIC) in jModeltest (Posada 2008). Log-likelihood values against generation time for each run were plotted in Tracer v1.7.1 (Rambaut *et al.* 2018). The first 25 % of the trees obtained were discarded as burn-in, and the remaining trees were used to construct a 50 % majority rule consensus tree and obtain the support for each clade as posterior probability (PP) values. Outgroups used in the phylogenetic analyses include taxa of Sigmodontinae and representatives of another rodents families (*i. e.*, Cricetidae, Nesomyidae and Spalacidae).

Studied specimens. We examined the external and craniodental morphology of 55 specimens of *Neomicroxus*, including skulls, skins, and fluid-preserved animals (see Appendix 1). Studied specimens are deposited in the following institutional collections: Argentina: Colección de Mamíferos del Centro Nacional Patagónico (CNP; Puerto Madryn, Chubut). Colombia: Colección de Mamíferos del Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH; Villa de Leyva, Boyacá). Colección de Mamíferos "Alberto Cadena García" del Instituto de Ciencias Naturales de la Universidad Nacional de Colombia (ICN: Bogotá). Colección de Mamíferos del Museo de Historia Natural de la Universidad Industrial de Santander (UIS-MZ; Bucaramanga, Santander). Ecuador: Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ; Quito). Instituto Nacional de Biodiversidad (INABIO–MECN; Quito). Instituto de Ciencias Biológicas de la Escuela Politécnica Nacional (MEPN; Quito). United States: National Museum of Natural History of Smithsonian Institute (USNM; Washington).

Morphometrics. Taking into account the important degree of hypsodonty showed by *Neomicroxus*, we established an ad-hoc classification composed by six tooth-wear stages (TWC, Figure 1), which based on dental wear on the cusps and the differentiation of the main structures. In this context, we considered as adults those specimens belonging to the TWC 4 to 6. These animals were employed in morphological qualitative assessment and ulterior statistical analyses based on 18 craniodental measurements (Appendix 4), taken with a digital caliper and expressed in millimeters. For descriptive purposes, univariate statistics for each measurement were calculated. To perform a multivariate exploration, we used a sample composed by 12 specimens of *N. bogotensis* and 21 of *N. latebricola* (sexes pooled) as input data for a principal component analysis (PCA; Johnson and Wichern 1999; Carleton and Musser 1989). Raw data were standardized by transformation to their natural logarithms and the first three principal components were calculated on the resultant covariance matrix. To test the potential variation of *N. bogotensis* through its range, we added to the analysis several Venezuelan speci-

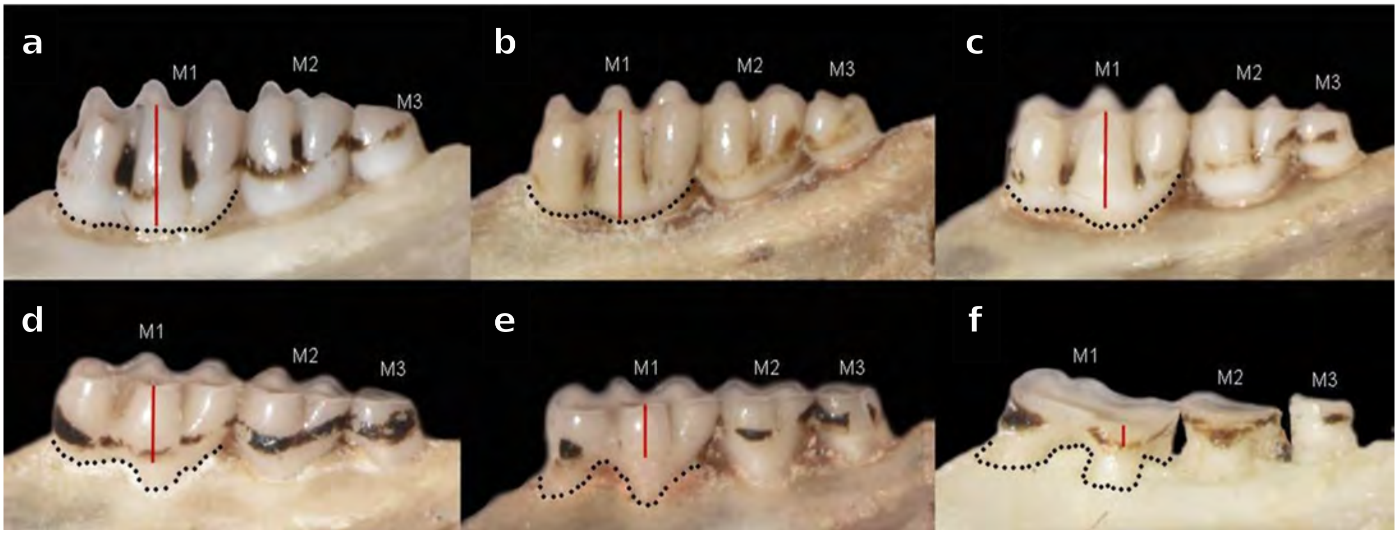


Figure 1. *Neomicroxus* age classification estimated by the dental wear on the cusps and the differentiation of the main structures. a) TWC1: M1-M2 cusps pronounced with flexus and fossettes visible. Features associated with the procingulum are notorious. M3 erupted, no wear, b) TWC2: M1-M2 similar to TWC1, but M3 shows slight wear worn although still complex in morphology, c) TWC3: M1 has a vestige of posteroloph, roots still are not very visible. M2 retaining some structures, but possesses some fossetes and vestige of the anteroloph. M3 structures are less distinguishable, d) TWC4: Smaller flexus and posteroloph in M1, with noticeable roots. M3 is almost flat with anteroloph and posteroloph barely visible or not distinguishable, e) TWC5: Molar surfaces with scarce occlusal structures, M1 anteromedian flexus not differentiated, M2 flexus slightly evident, and M3 fully flattened, and f) TWC6: Molar surfaces without occlusal structures, roots very visible. M3 is totally worn, clearly exposing the dentin.

mens (Mérida and Táchira states) with incomplete measurements because they were assessed with a different goal by the senior author. For this reason and to avoid calculations with missing data, we reduced the number of variables considered to eight (ONL, BZP, LD, LIF, LM1-3, BB, CIL, IML), and worked on a matrix composed by 12 individuals. For *N. latebricola*, the PCA was executed with 21 individuals and 18 variables (Appendix 3). Additionally, to assess the differentiation between the molecular recovered groups, we perform a Discriminant Analysis (DA) employing the same log-transformed data removing missing values (25 individuals, 16 variables). Group assignments were validated by a jackknife resampling. For all morphometrical analyses, we used the free software Past version 4.0 (Hammer *et al.* 2001).

Results

Phylogenetic relationships and genetic divergence. Phylogenetic analyses recovered well-resolved topologies within Oryzomyalia (*sensu* Steppan *et al.* 2004), with tribal relationships mostly concordant with previous studies (*e. g.*, Alvarado-Serrano and D'Elía 2013; Salazar-Bravo *et al.* 2016; Gonçalves *et al.* 2018). The genus *Neomicroxus* was found to be monophyletic with high support values (Figure 2a; BT1/BT2/PP = 99/99/1.0), but without affiliation to any recognized tribe in the MP and BI topologies, and sister to Abrotrichini + Wiedomyini in the ML analysis but weakly supported. In all approaches (MP, ML, and BI), two major clades strongly supported were retrieved within the genus. One clade is formed by individuals from Colombia (100/96/0.9) and can be referred to what is currently understood as *N. bogotensis*; another clade is represented by sequences from Ecuadorian Cordillera Oriental and Occidental (100/74/0.9), and can be confidently associated to *N. latebricola*. The overall mean divergence at the cytb gene for *Neomicroxus* reaches 6.3 %, meanwhile, the genetic distance between the two main clades is 11 % (see Appendix 3). In the *bogotensis* clade, the phyletic relationships show a profound divergence between individuals from Santander and Cundinamarca departments (> 6 %). Our sampling is insufficient to evaluate the demography of the species, however, the analyzed localities are geographically close, so we can affirm that the divergence observed between northern and central (Cundinamarca) Colombia is not due to a phenomenon of isolation by distance. This deep divergence (also reflected in the branch lengths), suggests that the populations of *N. bogotensis* here analyzed are older, possibly demographically stable, with a strong barrier (geographical or ecological) that interrupts gene flow.

On the other hand, within the *latebricola* clade, we recovered a shallow genealogy with two minor groups or subclades which diverge by 1.4 %. One subclade is composed of the same haplotype shared by QCAZ4160 and QCAZ4167 individuals, both from the Ecuadorian Napo province. Meanwhile the other subclade groups three different haplotypes, slightly divergent, from Carchi (MECN3727/MECN3734, QCAZ9801) and Napo (QCAZ4121) provinces (Appendix 3). Conversely to the observed variation in *N. bogotensis*, the genealogical relationships and the divergence values between and within *N. latebricola* subclades reveal the existence of current genetic flow between populations, reflected by the lack of reciprocal monophyly between the provinces, which also is a sign of populations in the process of expansion.

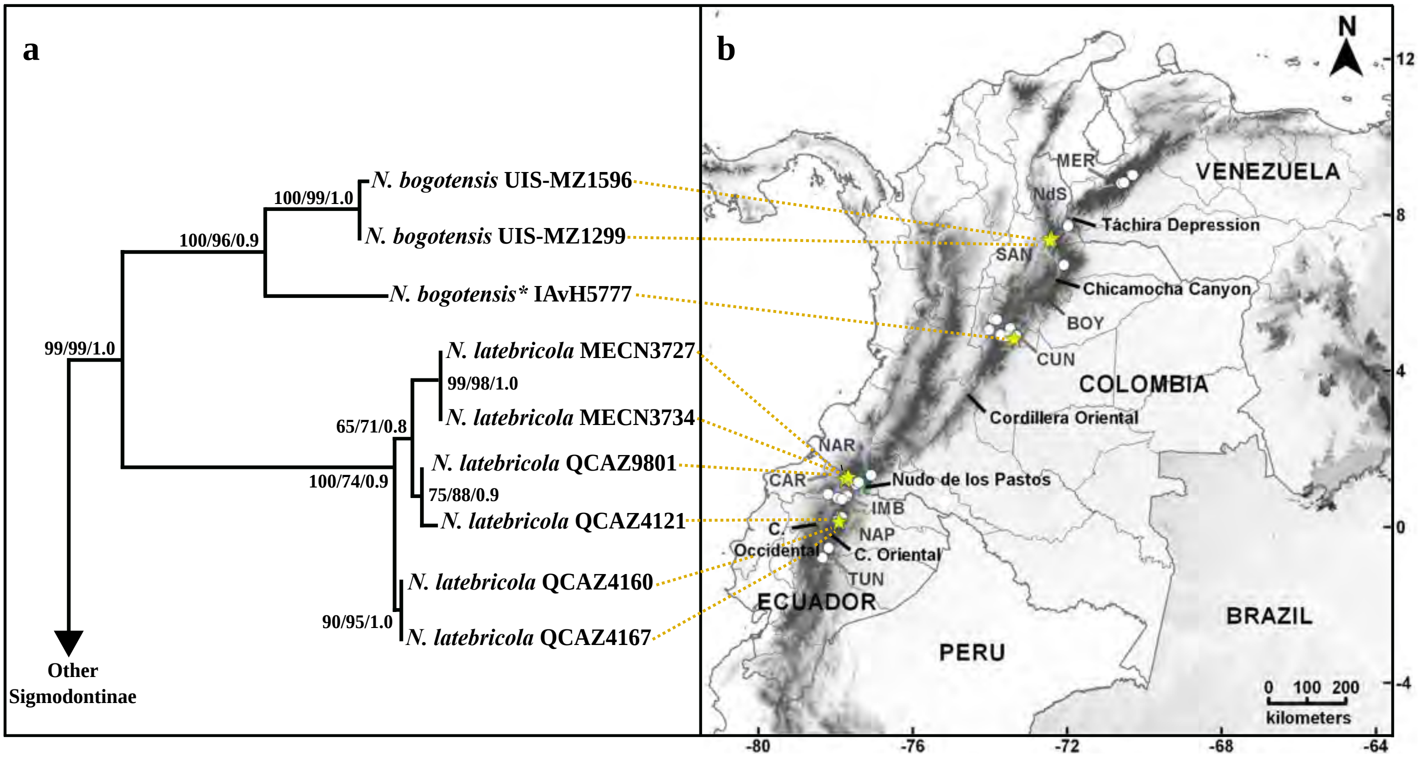
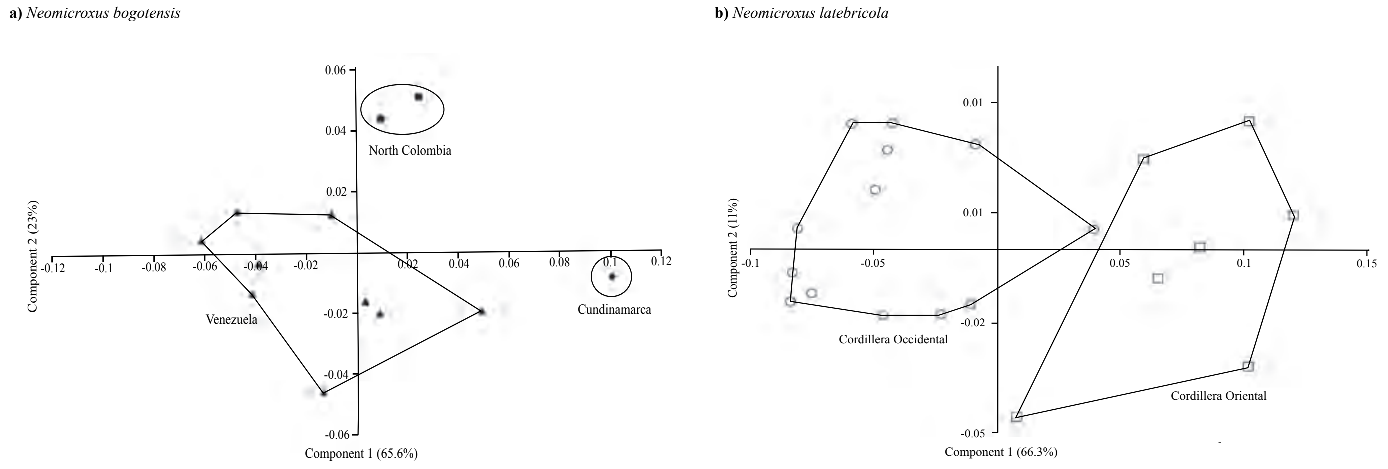


Figure 2. a) Phylogenetic tree of concatenated matrix related to the b) geographical distribution of *Neomicroxus* specimens from the Andes of Ecuador, Colombia and Venezuela. Support values (MP/ML/BI) are indicate next to each node. Yellow stars indicate specimens used in the phylogenetic analyses.

Morphometric analyses. The univariate morphometric analysis reveals little differences among the samples, being *N. bogotensis* who possesses lower values to several of the craniodental variables here recorded (Table 1). The PCA for *N. bogotensis* showed a clear separation between specimens from north of Colombia (Santander and Norte de Santander departments), Cundinamarca, and Venezuela (Figure 3). The 88.6 % of the total variation is summarized in the first two principal components, none of which can be interpreted as a size factor because they include positive and negative coefficients for some variables (Table 2). The largest contribution of the first component is attributed to the following variables: breadth of zygomatic plate, length of incisive foramina, length of upper diastema, occipitonasal length, while for the PC2 are the lengths of incisive foramina and the upper diastema. The *N. latebricola* PCA retrieves two partially overlapping groups from the Cordillera Oriental (Napo province) and Occidental (Carchi province; Figure 3). These results are congruent with the molecular results (see above); 77.2 % of the variation is explained by the PC1-2. The craniodental variables with the greatest contribution are the breadth of incisive foramina and breadth of the bony palate on the PC1, and breadth of zygomatic plate and length of incisive foramina on the PC2 (Table 2).

Table 1. Univariate statistics for selected craniodental measurements in *Neomicroxus*. Values provided are mean ± standard deviation and [minimum–maximum] range. All measurements are expressed in millimeters.

	***N. latebricola* Occidente**	***N. latebricola* Oriente**	***N. bogotensis* North Colombia**	***N. bogotensis* Cundinamarca**	***N. bogotensis* Venezuela**
	n = **13**	*n* = **9**	*n* = **3**	*n* = **1**	*n* = **9**
Occipitonasal length - ONL	25.53 ± 0.4 [24.95 - 26.21]	25.18 ± 0.22 [24.89 - 25.65]	23.52 ± 0.71 [22.75 - 24.14]	24.33	23.18 ± 0.39 [22.49 - 23.74]
Condylo-incisive length - CIL	23.18 ± 0.49 [22.49 - 23.91]	22.62 ± 0.24 [22.15 - 22.93]	20.57 ± 0.67 [19.9 - 21.24]	21.45	20.43 ± 0.31 [20.03 - 21.14]
Greatest zygomatic breadth - ZB	11.97 ± 0.15 [11.73 - 12.34]	12.04 ± 0.12 [11.82 -12.21]	–––	11.67	11.25 ± 0.21 [11.01 - 11.56]
Interorbital breadth - IB	4.70 ± 0.1 [4.41 - 4.87]	4.82 ± 0.12 [4.69 -5.06]	4.45 ± 0.19 [4.25 - 4.63]	4.75	–––
Breadth of zygomatic plate - BZP	1.39 ± 0.06 [1.3 - 1.5]	1.38 ± 0.1 [1.26 -1.52]	1.33 ± 0.04 [1.29 - 1.37]	1.67	1.36 ± 0.1 [1.23 -1.54]
Length of upper diastema - LD	6.26 ± 0.19 [6 - 6.68]	6.38 ± 0.2 [6.09 - 6.74]	5.75 ± 0.16 [5.58 -5.9]	6.01	5.6 ± 0.13 [5.39 - 5.83]
Breadth of bony palate - BBP	5.39 ± 0.1 [5.24 - 5.6]	5.36 ± 0.09 [5.26 - 5.51]	5.24 ± 0.35 [4.99 - 5.64]	5.59	–––
Length of incisive foramina - LIF	4.75 ± 0.18 [4.44 - 5]	4.73 ± 0.25 [4.46 - 5.15]	4.12 ± 0.71 [3.3 - 4.56]	4.5	3.97 ± 0.14 [3.76 - 4.17]
Breadth of incisive foramina - BIF	1.66 ± 0.1 [1.55 - 1.84]	2.02 ± 0.14 [1.83 - 2.2]	1.76 ± 0.13 [1.62 - 1.85]	1.87	–––
Length of maxillary toothrow - LM1-3	3.63 ± 0.1 [3.41 - 3.83]	3.5 ± 0.13 [3.26 - 3.69]	3.46 ± 0.06 [3.42 - 3.53]	3.73	3.57 ± 0.09 [3.43 - 3.69]
Breadth of first upper molar - BM	1.17 ± 0.04 [1.08 - 1.25]	1.12 ± 0.04 [1.03 - 1.17]	1.14 ± 0.09 [1.04 - 1.2]	1.15	–––
Breadth of palatal bridge - BPB	2.65 ± 0.16 [2.46 - 3.1]	2.99 ± 0.17 [2.75 - 3.31]	2.68 ± 0.49 [2.29 -3.23]	3.13	–––
Length of nasals - LN	10.11 ± 0.16 [9.66 - 10.27]	10.1 ± 0.12 [9.87 - 10.24]	9.24 ± 0.37 [8.84 - 9.58]	9.52	–––
Breadth of braincase - BB	11.65 ± 0.20 [11.21 - 11.96]	11.65 ± 0.15 [11.28 - 11.79]	10.93 ± 0.37 [10.53 -11.25]	11.26	11.11 ± 0.21 [10.72 - 11.38]
Breadth of the occipital condyles - BOC	6.14 ± 0.12 [5.92 - 6.39]	6.14 ± 0.09 [6.04 - 6.3]	5.82 ± 0.24 [5.55 - 5.98]	5.77	–––
Zygomatic internal length - ZIL	7.03 ± 0.17 [6.75 - 7.36]	7.08 ± 0.1 [6.85 - 7.18]	–––	6.61	–––
Mandibular length - ML	12.76 ± 0.33 [11.98 - 13.25]	13.04 ± 0.37 [12.6 - 13.59]	11.41 ± 0.29 [11.19 - 11.74]	12.15	–––
Mandibular molar toothrow length - IML	3.8 ± 0.08 [3.63 - 3.94]	3.65 ± 0.13 [3.43 - 3.78]	3.77 ± 0.03 [3.74 - 3.79]	3.87	3.77 ± 0.11 [3.63 - 3.9]


a) *Neomicroxus bogotensis*

b) *Neomicroxus latebricola*

Figure 3. Principal component analysis, components 1 and 2, of the 8 log-transformed craniodental measurements for in *N. bogotensis* (*n*=12), and 18 for *N. latebricola* (*n*=21). ♦: *N. bogotensis* Cundinamarca, ●: *N. bogotensis* North Colombia (Norte de Santander and Santander), ▲: *N. bogotensis* Venezuela, ○: *N. latebricola* Ecuadorian Cordillera Occidental, and □: *N. latebricola* Ecuadorian Cordillera Oriental.

The Discriminant Analysis confirms the separation of *N. bogotensis* from the north of Colombia *(i.e.* Norte de Santander and Santander departments) and the specimen of Cundinamarca department. Similarly, the samples of *N. latebricola* from the Oriental and Occidental cordilleras of Ecuador are clearly differentiated (Figure 4). For both species, the recovered groups are completely concordant with the molecular arrangements. According to jackknife resampling, the predefined groups (*i.e. N. bogotensis*: North Colombia [Norte de Santander and Santander departments], Cundinamarca, and Venezuela [Mérida], *N. latebricola*: Ecuadorian Cordillera Oriental and Occidental) are correctly classified in a 72 % when Venezuela is excluded, and a 70 % when it is included (Appendix 5). The variables which most contributed to the discrimination among these groups were the interorbital breadth, breadth of bony palate, breadth of incisive foramina, and breadth of first upper molar.

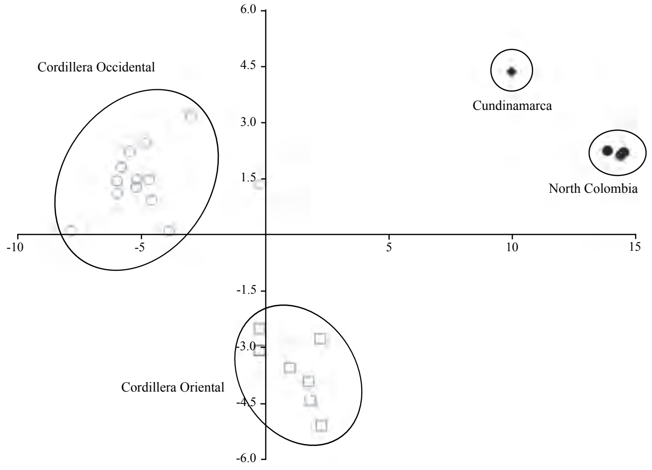


Figure 4. P Plot of canonical discriminant analysis based on 16 craniodental measurements from Colombian and Ecuadorian specimens of *Neomicroxus*. ♦: *N. bogotensis* Cundinamarca, ●: *N. bogotensis* North Colombia (Norte de Santander and Santander), ○: *N. latebricola* Ecuadorian Cordillera Occidental, and □: *N. latebricola* Ecuadorian Cordillera Oriental.

Discussion

Neomicroxus uniqueness and phylogeny. The distinction of *Neomicroxus* as a new entity was based on molecular data from a few specimens of *N. latebricola*, cemented with a shallow morphological review at generic level, mostly pointed to disconnect *Neomicroxus* from *Akodon* (Alvarado-Serrano and D'Elía 2013). Since then, only Curay (2019) ventured to evaluate the variability of *N. latebricola* studying several populationa samples in Ecuador. This approach highlighted the occurrence of *N. latebricola* in western locations from the cordillera Occidental, a finding previously reported by Brito (2013; overlooked in Alvarado-Serrano and D'Elía 2015) and revealed unsuspected geographical variation.

Despite these findings, the non-inclusion of *N. bogotensis* in a formal phylogenetic analysis has limited the confirmation of hypothesis advanced by Voss (2003) and Alvarado-Serrano and D'Elía (2013) about the generic status of *Neomicroxus*. The monophyly of *Neomicroxus* is not an unsuspected result since both species have been traditionally considered very close due to morphological similarity (Voss 2003). In turn, the novelty molecular data for *N. bogotensis*, added to those of *N. latebricola*, strengthens the consideration that the genus does not appear closely related to any other lineage, placing *Neomicroxus* as a Sigmodontinae *incertae sedis* (Alvarado-Serrano and D'Elía 2013). This finding invites to the recognition of a new clade on Andean rodents with tribal rank.

An additional issue is to explain the differential genealogical structure detected in each species of *Neomicroxus*, suggesting contrasting evolutionary histories. Probably, it could be linked with differential environmental conditions in the northern Andes along the Neogene that could promote the spatial structuring. Judged as a whole, the range of *Neomicroxus* shows an important gap in southern Colombia (Figure 2b). If this "lagoon," which turns sharply allopatric both species, is artefactual or real is debatable. Colombian southernmost portions to the Ecuadorian bor-

Table 2. Results of the principal component analysis based on measurements of *Neomicroxus* specimens. Scheme and names of taken measurements are illustrated in the Supporting information S3.

***N. bogotensis* (*n*=12)**

	PC 1	PC 2
ONL	0.18529	0.12481
BZP	0.79866	-0.51397
LD	0.23801	0.22664
LIF	0.46159	0.76969
LM1-3	0.1036	-0.25169
BB	0.004621	0.023879
CIL	0.19013	0.07015
IML	0.10575	-0.087326
Eigenvalue	0.0019788	0.0006965
% variance	65.571	23.081

***N. latebricola* (*n*=21)**

	PC 1	PC 2
ONL	-0.010971	0.11015
ZB	-0.006378	-0.025584
IB	0.09867	0.063224
BZP	0.041397	0.66519
LD	0.15393	0.24007
BBP	0.0086206	0.071494
LIF	0.067016	0.50184
BIF	0.78061	-0.11472
LM1-3	-0.096618	0.21955
BM1	-0.12144	0.16342
BPB	0.5329	0.031021
LN	0.024229	0.089939
BB	-0.018767	-0.077084
BOC	0.041391	-0.034099
CIL	-0.026062	0.19255
ZIL	0.074836	0.088529
MH	0.13971	0.20511
IML	-0.11945	0.18693
Eigenvalue	0.00417	0.00069
% variance	66.307	10.977

der have been largely controlled by armed forces, turning mammalogical surveys an almost impossible task. Since *N. latebricola* is recorded in Ecuador very close to this border, and taking into account the habitat continuity (Curay 2019), its occurrence in Colombia is highly expected. The Andean geography in southern Colombia is very complex involving, towards north of Nudo de los Pastos, the occurrence of three main chains (cordilleras) instead of the two branches characterizing the Ecuadorian Andes. We could assume that contact between populations of *N. latebricola* and *N. bogotensis* has been limited by factors associated with this complexity. However, the finding of a single specimen from Nariño, Pasto Municipality, (Ramírez-Chaves and Noguera-Urbano 2010), which was erroneously identified as *N. latebricola* (Appendix 6), evidences that the distribution of *bogotensis* extends to the south of Colombia, and supports our hypothesis of reduced sampling in the region.

Neomicroxus bogotensis spatial structure and taxonomic implications. Of the two species currently considered in *Neomicroxus*, *N. bogotensis*, the smallest in body size, is the most poorly known. Almost a century after its shallow original description (Thomas 1895), *N. bogotensis* received some attention. Reig (1987:360) concluded, after the inspection of its holotype, that *bogotensis* belongs "… *neither to* Akodon *nor to* Abrothrix *and that is a distinctive genus of Akodontini*." In addition, provided an informal diagnosis of *Microxus*, the genus where he placed this form, and distinguished *bogotensis* by their unique diploid complement (2n = 35-37, FN = 48; Barros and Reig 1979), and the lacking of paired ventral prostates (shared with *Thaptomys*, a finding conducted by Voss and Linzey 1981). The most recent descriptions of the species (Alvarado-Serrano and D'Elía 2015:98; Pardiñas and Brito 2017:409) considered this taxon as monotypic, despite previous indications in opposite way (see below).

Although stated as "rare" (see Linares 1998:272; Alvarado-Serrano and D'Elía 2015:98), *N. bogotensis* is an abundant cricetid in Andean highlands, at elevations between 2,400 and 3,900 masl, which corresponds to the cloud forest and páramo ecosystems (Cuatrecasas 1958; López-Arévalo *et al.* 1993; Rangel 2001). Ecological and systematic studies report it as an easy species to found in evergreen ombrophile montane forest and shrubby upland meadows (*e. g.*, Reig 1986; López-Arévalo *et al.* 1993; Soriano *et al.* 1999; Ventura *et al.* 2000; Vianchá *et al.* 2012).

Originally described for the "Plains of Bogota" (Thomas 1895:369), Cundinamarca, it has also been collected in others departments associated with the Cordillera Oriental in Colombia as Boyacá, Santander, and Norte de Santander (Saénz-Jiménez 2010; Vianchá *et al.* 2012). Some databases of mammalian collections also list specimens, not reviewed in this contribution, from the departments of César, Tolima, and Huila (*i. e.,* American Museum of Natural History, The Field Museum of Natural History). The record of Ramírez-Chaves and Noguera-Urbano (2010) from the Nariño department is a significant data about the extension of the *N. bogotensis* geographic range towards southern Colombia. The range for the species is completed by its occurrence in the Cordillera de Mérida and Páramo de Tamá, in the Venezuelan states of Táchira and Mérida (Alvarado-Serrano 2005), plus an unconfirmed mention from Trujillo (Soriano *et al.* 1999).

Our analyses revealed a clear geographic structure in *N. bogotensis*, separating with strong support the specimens of Norte de Santander and Santander from that of Cundinamarca. Although our study has only a sequence of Cundinamarca, the high genetic distance values (> 6%) suggest the specific distinction of the populations from northern Colombia. This also warns about the restricted gene flow between northern departments and Cundinamarca.

It is interesting to note that so far, no studies have evaluated populations in northern Colombia and Venezuela as a whole. Soriano *et al.* (1999) highlight the need to examine the taxonomic identity of the populations of *N. bogotensis* in Venezuelan Andes. According to these authors, "*it is convenient to examine the taxonomic identity of the populations of the latter* [Neomicroxus bogotensis], *in the light of the parapatric or gradient speciation model, as has been referred to by Patton et al. (1990). Thus, given its high Andean distribution pattern, we expect that the morphotype of the Cordillera de Mérida, by virtue of its possible geographical isolation, could be distinguishable from the rest of the Andean populations. In the same way, we think that the identity of the Venezuelan populations of* T.[homasomys] laniger *and* Chilomys instans *would have to be examined*" (Soriano *et al.* 1999:22).

The Andes in northern Colombia and Venezuela have great geographical complexity characterized by some depressions (*e. g.*, Táchira and Barquisimeto Depression) that separate the mountains and generate significant breaks that lead to isolation and formation of so-called "montane sky islands" (Reig 1986; Anderson *et al.* 2012). In this sense, the Táchira Depression, characterized by a dry subtropical climate, has been regarded as a biogeographical barrier to the dispersal of Andean species from both cordilleras (Cordillera Oriental de Colombia and Cordillera de Mérida, Soriano *et al.* 1999; Soriano *et al.* 2005). Species with lower vagility and strictly restricted to the cloud forest and páramo, would be virtually absent today, but probably had a wider and continuous distribution during glacial periods as suggested for *Heteromys australis* (Anderson and Soriano 1999) and *Marmosa waterhousei* (Gutiérrez *et al.* 2011), both species distributed in a lower altitudinal range than *Neomicroxus*. Based on the morphometrical results, the individuals from Venezuela are smaller (Figure 3, Table 1), clearly distinguishable from the Colombian specimens. It seems unlikely that the absence of *N. bogotensis* in the Táchira Depression is just an artifact of inadequate sampling. Probably, the current climatic conditions of this geographical barrier are too dry and would be an inadequate habitat for a typical species of cloud forest and páramo environments, which would restrict gene flow between Colombian and Venezuelan populations. In this way, a study with greater geographical coverage could favor the predictions of Soriano *et al*. (1999).

Our preliminary data from populations of the Norte de Santander and Santander add diversity to the current concept of *N. bogotensis* in Colombia. The high divergence level suggests a deep break between specimens from northern Colombia and Cundinamarca (the department where the type locality is placed; Thomas 1895). An important geographic barrier of this area is the Chicamocha canyon produced by the erosion of the tributary of Chicamocha river through the Boyacá and Santander departments, and it has been referred to as responsible for the allopatric speciation in some small vertebrates (*e. g.*, Guarnizo *et al.* 2015; Cárdenas 2017). Unpublished data from one of the authors (JCP) also suggests a high divergence degree on cytb sequences in *Cryptotis thomasi*, *Thomasomys niveipes* and *Notosciurus granatensis* from both sides of this barrier.

Although *N. bogotensis* has only been formally mentioned for Cundinamarca, Boyacá and Santander departments (Saénz-Jiménez 2010; Vianchá *et al.* 2012), is very probably that the species occurs in the Cordillera Oriental and extends its distribution southward. In this sense, the record of Ramírez-Chaves and Noguera-Urbano (2010) from Nariño, support this assumption and suggest that the museum specimens from Tolima, Huila and Cauca would correspond to *N. bogotensis*. So, the gap that we observe in the distribution of this species is probably due to insufficient sampling and both *Neomicroxus* species would not be allopatric.

Our findings expose key points to consider in future studies: i) the diversity of *N. bogotensis* seems greater than that reflected in its current concept, ii) topographic and climatic complexity are playing an important role in the diversification of small Andean mammals being probably responsible for the observed genetic discontinuities, especially in the northern Andes of Colombia, iii) as a way of clarifying the gap observed towards southern Colombia and bordering Ecuador, is necessary to focus the sampling efforts towards regions still unexplored, iv) the review of specimens deposited in collections that were not evaluated in this work is imperative, and v) the importance of future studies that evaluate the Colombian and Venezuelan populations as a whole.

Neomicroxus latebricola *spatial structure and taxonomic implications. N. latebricola* was originally described from a single specimen from Tungurahua province in central Ecuador (Anthony 1924). A few additional studies have extended its distribution to include Napo, Pichincha, Imbambura, and Carchi provinces as well as revealed findings like a shallow geographical structure (Curay 2019; Voss 2003; Alvarado-Serrano 2005; Brito 2013). Additionally, Muñoz *et al.* (2018) determined a chromosomal number of 2n = 44, FN = 42, for specimens from Pirámides de Cochasqui, Cantón Pedro Moncayo, Pichincha province. Similar to *N. bogotensis*, *N. latebricola* is a common and abundant species easy to capture in *Polylepis* forests and páramo between 2,420 and 3,950 masl (Brito 2013;Curay 2019).

Our molecular phylogenetic analysis confirms the structure observed with the morphometric dataset, which shows a partial overlapping between specimens from along both cordilleras in Ecuador. This overlapping is reflected in the genealogical relationships between individuals from Carchi and a specimen from Napo province, which could be evidence of an area of primary or secondary contact. A primary contact zone implies the differentiation of the population in situ, while the secondary is produced by the contact of previously allopatric populations (*e. g.*, Schneider 1996; Bertl *et al.* 2018). For now, our data are insufficient to distinguish between these two scenarios.

The variation observed within *N. latebricola* allows to highlight two important points: i) the measurements of the specimens from Cordillera Oriental fit into the metric variation recorded by Anthony (1924) and later authors (Moreno and Albuja 2005; Alvarado-Serrano and D'Elía 2013), and ii) the potential distinction of a new subspecies for the Cordillera Occidental populations, distinguished from the nominotypic form by a summatory of craniodental traits and coloration. In fact, Curay (2019) notes variations in the dorsoventral coloration of the body and the forefoot and hindfoot, which could be related to the habitats characteristics (*e. g.*, topography, climate, vegetation) in both cordilleras. Our geographic coverage allows us to state that *N. latebricola* in the Cordillera Occidental is a frequent species, strictly associated to forests with shrubs and trees where *Polylepis incana* is the dominant plant (Brito 2013). By the contrary, *N. latebricola* in the Cordillera Oriental occurs in the ecotonal zone between the páramo and forest whose typical vegetation is the wiry bunch grass to 1 m high and other larger species frequent of wooded environments (Voss 2003). The intraspecific color variation in rodents has been associated with the sex, age, seasonality, and habitat (*e. g.*, Camargo *et al.* 2016; Ríos and Álvarez-Castañeda 2012; Sandoval *et al.* 2016). In this regard, the coloration pattern in *N. latebricola* seems linked with the soil and vegetation color and the exposure to be detected by predators. It varies from darker in the open habitat from the Cordillera Oriental to light brownish in the habitat with more vegetation coverage in the Cordillera Occidental.

Related to the molecular data, the shallow topology (Figure 2a), shared haplotypes, and low genetic distance values reveal the existence of current genetic flow among its populations suggesting there are no apparent geographical barriers that limit it. Contrary to what we have inferred for *N. bogotensis* populations, *N. latebricola* has experienced recent demographic expansion. These results imply that the geographic complexity of the Ecuadorian Andes is not a determining factor in the differentiation of these populations.

The presumptive existence of a new infraspecific taxon within *N. latebricola* implies raising the wide debate over the importance and utility of the subspecies (*e. g.*, Wilson and Brown 1953; Endler 1977; Fitzpatrick 2010). The traditional concept involves geographic discontinuities on some morphological traits within a species as the result of ecological and historical factors, but the constant search for agreement between morphological and molecular data has led to an incorrect interpretation of what subspecies would be. Based mainly on DNA data, many authors have equated obtaining geographic structure and reciprocal monophyly, used to delineate species, as useful and appropriate ways to identify or to reject subspecies. However, this goes against the gene flow that exists between the populations of a species and that maintains them as a clear taxonomic unit. The geographic variation recovered in *N. latebricola* reminds us of the statement of Patton and Conroy (2019:1019) about the subspecies "*… are genealogical networks of populations, often without cladistics structure…*" instead the species are considered "*…hierarchical units with a dichotomous branching history.*" This conceptual distinction is key to improve the understanding that species and subspecies are not equivalent, and that this misunderstanding has caused us to ignore or obscure the infraspecific diversity of taxa. In this case, our data clearly support the existence of a new subspecies for *N. latebricola* such a typical inhabitant of the forests of *Polylepis*.

Conflicts between molecular data and morphological evidence, especially the necessity to find data congruence and monophyly, and the attempt to delineate molecular clades with phenotypical features, triggered the progressive discard of infraspecific treatments and its biological value. Paradigmatic examples are abundant among Patagonian sigmodontines with prolific nominal contents (*e. g., Abrothrix*, *Loxodontomys, Oligoryzomys*, *Paynomys*; see Palma *et al.* 2010; Cañón *et al.* 2010; Alarcón *et al.* 2011; Palma and Rodríguez-Serrano 2017). Clearly, we need to reevaluate large series of specimens, looking for diagnosable patterns of size and color in accordance with geography, in a refoundational effort to recover the value of geographic races among South American cricetids.

Finally, despite the verifiable progress during last decades there is a remarkable lack of basic knowledge affecting many Andean sigmodontines (*e. g.*, *Aepeomys lugens*, *Chilomys instans*, several *Thomasomys*). *Neomicroxus* is a crystal example for which many aspects of its natural history, ecology, biogeography and alpha taxonomy still remain unknown. Our contribution set a preliminary base for future studies evaluating the variation within the genus, as well as that of other small non-volant mammals with shared distributions. On the other hand, it exposes the importance of the subspecies concept such as nonhierarchical, nonreciprocal monophyletic, closely interbreed, and geographically structured groups.

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Appendix 1

Specimens examined in the morphologic and genetic analyses. Genbank access numbers of the five sequenced specimens in this study are indicated in bold. * Cytb, ** IRBP

N. bogotensis: COLOMBIA: 1) Boyacá, Municipio Guacamayas, vereda Alfaro, sitio Piedras Blancas 6.416, -72.505 (ICN 14722). 2) Cundinamarca, Junín, Reserva Biológica Carpanta 4.563, -73.683 (ICN 11027, ICN 11028, ICN 11029). 3) Cundinamarca, PNN Chingaza (IAvH 5777 - **MT240521***). 4) Nariño, Pasto, aproximadamente 15 km carretera Pasto-Mocoa, páramo, cabaña La Pastora 0.866, -77.316 (ICN13284). 5) Norte de Santander, Cucutilla, Sisavita, Romeral, Predio Greystar [no coordinates] (UIS-MZ 907). 6) Santander, Santa Bárbara, Páramo del Almorzadero, Vereda Volcanes 7.076, -72.848 (UIS-MZ 1596 - **MT240520* MT249798****). 7) Santander, Santa Bárbara, Vereda Esparta 7.019, -72.892 (UIS-MZ 1299 - **MT240522* MT249797****), VENEZUELA: 8) Mérida, Tabay, 7 Km SE Tabay, La Coromoto 8.6, -71.02 (USNM 374611, USNM 374612, USNM 374613).

N. latebricola: ECUADOR: 1) Carchi, Espejo, La Libertad, Sector Bosque de *Polylepis* 0.712202, -77.981639, 3650 (MECN 3717-19, 3727 - **MT240523* MT249799****, 3734 – **MT240524* MT249800****, 3735-36, 3739-40, 3748, 4376-77; QCAZ 11142, 11158, 11145, 12504, 12503, 9814; MEPN 10869, 10870, 10887, 10886, 12716, 10644, 12718, 12715B, 10485, 12712, 12715). 2) Carchi, Tulfán, Tufiño, Páramo del Artesón, Comuna La Esperanza (QCAZ 9801). 3) Imbabura, Pimampiro, Mariano Acosta, Laguna Blanca 0.22367, -77.97867, 3400 msnm (MECN 4763). 4) Imbabura, Zuleta, Faldas del Imbabura 0.248372, -78.15425, 3610 msnm (MECN 6134-36). 4) Imbabura, Cotacachi, Bosque Protector Neblina 0.342024, -78.412935, 2990 msnm (MECN 5605-06). 5) Napo, Quijo, bosque administrado por la fundación TERRA -0.33422, -78.1433, 3400 msnm (QCAZ 4090, 4121, 4160, 4167, 5230, 5236, 5239). 6) Tunguragua, Pisayambo, km. Parque Nacional Llanganates -1.044686, -78.345828, 3102 msnm (CNP 6396 - MECN 1739).

Appendix 2

List of taxa for which DNA sequences were included in the phylogenetic analysis. GenBank accession numbers and vouchers for mitochondrial and nuclear genes are indicated.

Species	Cytochrome b Access number	Cytochrome b Voucher	IRBP Access number	IRBP Voucher
Abrawayaomys chebezi	KR069109	CG184	MN969035	CG184
Abrawayaomys ruschii	JX949189	MN67557	JX949185	MN67557
Abrothrix hirta	U03530	MVZ154494	KC953347	MVZ154494
Aegialomys xanthaeolus	EU074632	TK135790	EU273420	TK135790
Aepeomys lugens	–––	–––	DQ003722	MNHN4350
Akodon boliviensis	M35691	MVZ171607	KC953351	FMNH162747
Amphinectomys savamis	EU579480	MV97005	AY163579	MV970045
Andalgalomys pearsoni	JQ434418	MSB80512	JQ434398	MSB80512
Andinomys edax	JQ434419	MSB70545	JQ434399	MSB70545
Arvicola terrestris	AY275106	MVZ155884	AY277407	MVZ155884
Auliscomys sublimis	JQ434421	MSB75260	JQ434402	MSB75260
Baiomys musculus	EF989933	ROM97641	KC953360	ROM JM48
Bibimys labiosus	DQ444329	MN62062	AY277436	MN62062
Blarinomys breviceps	AY275112	CIT1391	AY277437	CIT1391
Brucepattersonius soricinus	AY277486	MVZ183036	AY277438	MVZ183250
Calassomys apicalis	JQ434425	GDE2012	KX431561	?
Calomys laucha	AY033190	NK72376	JQ434404	MSB80539
Castoria angustidens	EF622508	?	KF815411	MN78921
Cerradomys subflavus	EU579481	MNRJ61885	AY163626	MNRJ61665
Chelemys megalonyx	DQ309559	NK109208	EU091259	NK109253
Chilomys instans	AF108679	JLP16693	–––	–––
Chinchillula sahamae	JQ434422	MSB75154	JQ434409	MSB75254
Clethrionomys gapperi	AY309431	?	AY326080	UMMZ162467
Cricetulus longicaudatus	KM067270	?	AY326082	USNM449102
Cricetus cricetus	AJ490302	?	AY277410	MVZ155880
Delomys dorsalis	KF317031	JFV226	KC953369	MVZ182789
Deltamys kempi	AY195862	MNHN4151	AY277444	MNHN4151
Drymoreomys albimaculatus	EU579487	MVZ182088	EU649042	MVZ182088
Eligmodontia typus	AF108692	MVZ182681	AY277445	MVZ182681
Eremoryzomys polious	EU579483	FMNH129243	AY163624	FMNH129243
Euneomys chinchilloides	AY275115	UP LB018	AY277446	UPLB018
Euryoryzomys macconnelli	GU126538	AMNH272669	AY163620	AMNH272678
Galenomys garleppi	JQ434423	AMNH262814	JQ434410	AMNH262814
Geoxus valdivianus	AY275116	CAV001	AY277448	CAV001
Graomys griseoflavus	AY275117	UP278	AY277449	UP278
Handleyomys alfaroi	EU579489	TK93700	EU649044	TK93700
Handleyomys intectus	EU579490	CADV088	AY163584	ICN16093
Holochilus brasiliensis	GU126517	GD081	AY163585	GD081
Hylaeamys megacephalus	EU579499	MHNLS8061	AY163621	MHNLS8061
Irenomys tarsalis	U03534	MVZ155839	AY277450	MVZ155839
Isthmomys pirrensis	DQ836298	?	EF989847	ROM116309
Juliomys pictipes	FJ026733	TK145073	KC953385	MVZ182079
Juscelinomys huanchacae	AY275119	LHE1617	AY277452	LHE1616
Kunsia tomentosus	AY275121	LHE1620	KC953386	USNM584516
Lenoxus apicalis	U03541	MVZ171512	KC953388	MVZ171512
Loxodontomys micropus	AY275122	EPU001	AY277457	EPU001
Lundomys molitor	JQ966241	MCNU2302	JQ966805	MCNU2302
Megalomys desmarestii	LN810053	NHMUK1850	–––	–––
Melanomys caliginosus	EU340020	TK135894	KC953397	USNM464387
Mesocricetus auratus	AM904612	MauCytb06	AY163591	?
Microakodontomys transitorious	–––	–––	EU649054	MN25969
Microryzomys minutus	AF108698	MVZ173975	AY163592	MVZ166666
Microtus californicus	EF506105	MVZ216595	KC953401	MVZ207423
Myospalax aspalax	AF326272	?	AY326097	MSB100576
Neacomys spinosus	EU579504	MVZ155014	AY163597	MVZ155014
Necromys amoenus	AY273911	MVZ171563	AY277458	MVZ171569
Nectomys squamipes	GU126522	FMNH141632	EU273419	TK63841
Neomicroxus bogotensis	MT240520	UIS-MZ 1596	MT249798	UIS-MZ 1596
Neomicroxus bogotensis	MT240521	IAvH5777	–––	–––
Neomicroxus bogotensis	MT240522	UIS-MZ 1299	MT249797	UIS-MZ 1299
Neomicroxus latebricola	HQ731489	QCAZ4121	–––	–––
Neomicroxus latebricola	HQ731488	QCAZ9801	–––	–––
Neomicroxus latebricola	HQ731490	QCAZ4167	KF437367	QCAZ4167
Neomicroxus latebricola	KF437365	QCAZ4160	KF437366	QCAZ4160
Neomicroxus latebricola	MT240523	MECN3727	MT249799	MECN3727
Neomicroxus latebricola	MT240524	MECN3734	MT249800	MECN3734
Neotoma floridana	AF294344	TK52115	KC953411	OSU OK 107
Neotomys ebriosus	JQ434424	MSB87134	JQ434413	MSB87134
Nephelomys albigularis	EU579505	AMNH268125	AY163614	AMNH268125
Nesomys rufus	AF160592	Nruf508	AY326099	FMNH151915
Nesoryzomys swarthi	EU340014	ASNHC10003	AY163601	ASNHC10003
Neusticomys monticolus	KF359515	ACUNHC900	KR105605	QCAZ6531
Nyctoms sumichrasti	AY195801	TK101875	KC953421	MSB45815
Oecomys concolor	JF693876	MVZ155005	KC953424	MVZ192947
Oligoryzomys fulvescens	GU126529	AMNH257262	AY163611	AMNH257262
Onychomys leucogaster	EF989959	ROM114892	EF989860	ROM114892
Oreoryzomys balneator	EU579510	AMNH268144	AY163617	AMNH268144
Oryzomys palustris	GU126539	TTU75311	AY163623	TTU75311
Ototylomys phyllotis	AY009789	FN32783	KC953429	ROM35529
Oxymycterus nasutus	EF661854	?	AY277468	MVZ182701
Paynomys macronyx	U03533	MVZ155800	AY277441	MVZ155800
Pennatomys nivalis	LN810055	B5 534	–––	–––
Peromyscus leucopus	EF989979	ROM101861	EF989880	ROM101861
Phaeomys ferrugineus	KM065876	MZUFV3400	KM065877	MZUFV3400
Phodopus sungorus	AJ973390	?	KC953439	?
Phyllotis xanthopygus	U86833	MFS1324	AY163632	MVZ182703
Podoxymys roraimae	KM816650	PK3335	KM816651	PK3335
Pseudoryzomys simplex	GU126547	GD065	AY163633	GD065
Punomys kofordi	JQ434426	VPT 1890	JQ434414	VPT1890
Reithrodon auritus	EU579474	MVZ182704	AY163634	MVZ182704
Reithrodontomys fulvescens	EF990003	ROM114901	EF989904	ROM114901
Rhagomys longilingua	KY754141	?	DQ003723	FMNH175218
Rheomys raptor	KJ921706	KU159017	KC953451	ROM101294
Rhipidomys macconnelli	AY275130	MVZ 160082	AY277474	MVZ160082
Salinomys delicatus	EU377608	OMNH23602	JQ434415	OMNH23602
Scapteromys tumidus	AY275133	MVZ183269	AY277477	MVZ193269
Scolomys ucayalensis	EU579518	AMNH272721	AY163638	AMNH272721
Scotinomys teguina	AF108705	UMMZ3373	AY277415	MVZ191230
Sigmodon hispidus	AF425227	TK90616	AY277479	NK27055
Sigmodontomys alfari	EU074635	USNM449895	AY163641	USNM449895
Sooretamys angouya	GU126534	MNRJ50234	KC953456	MVZ192961
Tanyuromys aphrastus	JF693877	KU161003	JF693878	KU161003
Tapecomys wolffsohni	U86834	MSB67270	KC953460	MSB63364
Thalpomys cerradensis	AY273916	MZUSP30397	AY277480	MZUSP30400
Thaptomys nigrita	AF108666	MVZ183044	AY277482	MVZ183044
Thomasomys aureus	U03540	MVZ170076 & 166714	AY277483	MVZ170076
Transandinomys talamancae	GU126544	USNM449894	KC953465	MSB91815
Tylomys nudicaudus	DQ179812	TK41551	AY163643	ROM103590
Wiedomys pyrrhorhinos	EU579477	MVZ197566	AY277485	MVZ197567
Wilfredomys oenax	KJ663726	UFSM619	KJ663727	MCNU2025
Zygodontomys brevicauda	GU126549	AMNH257321	AY163645	AMNH257321

Appendix 3

Genetic divergence values (*p* distance) among cytochrome b sequences of *Neomicroxus.*

Overall mean	*Neomicroxus* genus p dist	%
Neomicroxus genus	0.063	6.3

Pairwise differences	***Neomicroxus* p distance** UIS-MZ 1596	IAvh5777	UIS-MZ 1299	QCAZ4160	QCAZ4167	QCAZ4121	QCAZ9801	MECN3727
UIS-MZ 1596 Nbogotensis								
IAvH5777 Nbogotensis	0.065							
UIS-MZ 1299 Nbogotensis	0.001	0.061						
KF437365 Nlatebricola QCAZ4160	0.107	0.113	0.107					
HQ731490 Nlatebricola QCAZ4167	0.107	0.112	0.106	0.000				
HQ731489 Nlatebricola QCAZ4121	0.109	0.112	0.109	0.014	0.014			
HQ731488 Nlatebricola QCAZ9801	0.109	0.110	0.109	0.010	0.010	0.004		
MECN3727 Nlatebricola	0.113	0.114	0.113	0.016	0.016	0.015	0.011	
MECN3734 Nlatebricola	0.113	0.114	0.113	0.016	0.016	0.015	0.011	0.000

Pairwise differences	***Neomicroxus* percentage** UIS-MZ 1596	IAvh5777	UIS-MZ 1299	QCAZ4160	QCAZ4167	QCAZ4121	QCAZ9801	MECN3727
UIS-MZ 1596 Nbogotensis								
IAvH5777 Nbogotensis	6.522							
UIS-MZ 1299 Nbogotensis	0.127	6.089						
KF437365 Nlatebricola QCAZ4160	10.673	11.268	10.652					
HQ731490 Nlatebricola QCAZ4167	10.673	11.215	10.625	0.000				
HQ731489 Nlatebricola QCAZ4121	10.928	11.215	10.875	1.377	1.373			
HQ731488 Nlatebricola QCAZ9801	10.928	10.981	10.875	1.001	0.999	0.375		
MECN3727 Nlatebricola	11.309	11.449	11.250	1.627	1.623	1.498	1.124	
MECN3734 Nlatebricola	11.309	11.449	11.250	1.627	1.623	1.498	1.124	0.000

Between species	**p dist** *N. bogotensis*	**%** *N. bogotensis*
N. bogotensis		
N. latebricola	0.111	11.051

Overall mean	**p dist**	**%**
N. bogotensis	0.042	4.2

Pairwise differences	***N. bogotensis* p distance** UIS-MZ 1596	IAvh5777
UIS-MZ 1596 Nbogotensis		
IAvH5777 Nbogotensis	0.065	
UIS-MZ 1299 Nbogotensis	0.001	0.061

Pairwise differences	***N. bogotensis* pecentage** UIS-MZ 1596	IAvh5777
UIS-MZ 1596 Nbogotensis		
IAvH5777 Nbogotensis	6.522	
UIS-MZ 1299 Nbogotensis	0.127	6.089

Overall mean	**p dist**	**%**
N. latebricola	0.011	1.1

Pairwise differences	***N. latebricola* p distance** QCAZ4160	QCAZ4167	QCAZ4121	QCAZ9801	MECN3727
KF437365 Nlatebricola QCAZ4160					
HQ731490 Nlatebricola QCAZ4167	0.000				
HQ731489 Nlatebricola QCAZ4121	0.014	0.014			
HQ731488 Nlatebricola QCAZ9801	0.010	0.010	0.004		
MECN3727 Nlatebricola	0.016	0.016	0.015	0.011	
MECN3734 Nlatebricola	0.016	0.016	0.015	0.011	0.000

Pairwise differences	***N. latebricola* percentage** QCAZ4160	QCAZ4167	QCAZ4121	QCAZ9801	MECN3727
KF437365 Nlatebricola QCAZ4160					
HQ731490 Nlatebricola QCAZ4167	0.000				
HQ731489 Nlatebricola QCAZ4121	1.377	1.373			
HQ731488 Nlatebricola QCAZ9801	1.001	0.999	0.375		
MECN3727 Nlatebricola	1.627	1.623	1.498	1.124	
MECN3734 Nlatebricola	1.627	1.623	1.498	1.124	0.000

Between clades *N. latebricola*	**p distance**	**%**
N. latebricola clade 1 [Napo]		
N. latebricola clade 2 [Carchi & Napo]	0.014	1.406

Within clades *N. latebricola*	**p distance**	**%**
N. latebricola clade 1 [Napo]	0	0
N. latebricola clade 2 [Carchi & Napo]	0.009	0.936

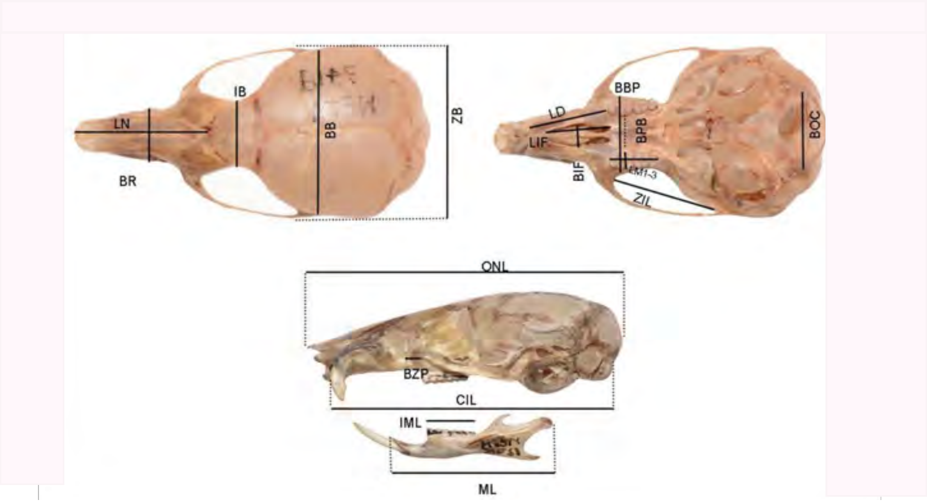
Between subcl - clade 2 *N. latebricola*	**p distance** **subcl. 1**	**%** **subcl. 1**
latebricola clado 2 subclado 1		
latebricola clado 2 subclado 2	0.013	1.311

Whitin subcl- clade 2 *N. latebricola*	**p distance**	**%**
latebricola clade 2 subclade 1	0.004	0.375
latebricola clade 2 subclade 2	0.000	0.000

	N. latebricola		**Locality**
Clade 1	QCAZ4160		Ecuador, Napo, Papallacta, bosque administrado por la fundación TERRA
	QCAZ4167		Ecuador, Napo, Papallacta, bosque administrado por la fundación TERRA
Clade 2	subclade 1	QCAZ4121	Ecuador, Napo, Papallacta, bosque administrado por la fundación TERRA
		QCAZ9801	Ecuador, Carchi, Tulfán, Tufiño, Páramo del Artesón, Comuna La Esperanza
	subclade 2	MECN3727	Ecuador, Carchi, Espejo, La Libertad, Sector Bosque de Polylepis
		MECN3734	Ecuador, Carchi, Espejo, La Libertad, Sector Bosque de Polylepis

Appendix 4

Linear measurements used in descriptive, univariate, and multivariate analyses.



BB Breadth of braincase, **BIF** Breadth of incisive foramina, **BM** Breadth of first upper molar, **BBP** Breadth of bony palate, **BPB** Breadth of palate bridge, **BOC** Breadth of the occipital condyles, **BZP** Breadth of zygomatic plate, **CIL** Condylo-incisive length, **IB** Interorbital breadth, **IML** Mandibular molar toothrow length, **LD** Length of upper diastema, **LIF** Length of incisive foramina, **LM1-3** Length of maxillary toothrow, **LN** Length of nasals, **ML** Mandibular length, **ONL** Occipitonasal length, **ZB** Greatest zygomatic breadth, **ZIL** Zygomatic internal length.

Appendix 5

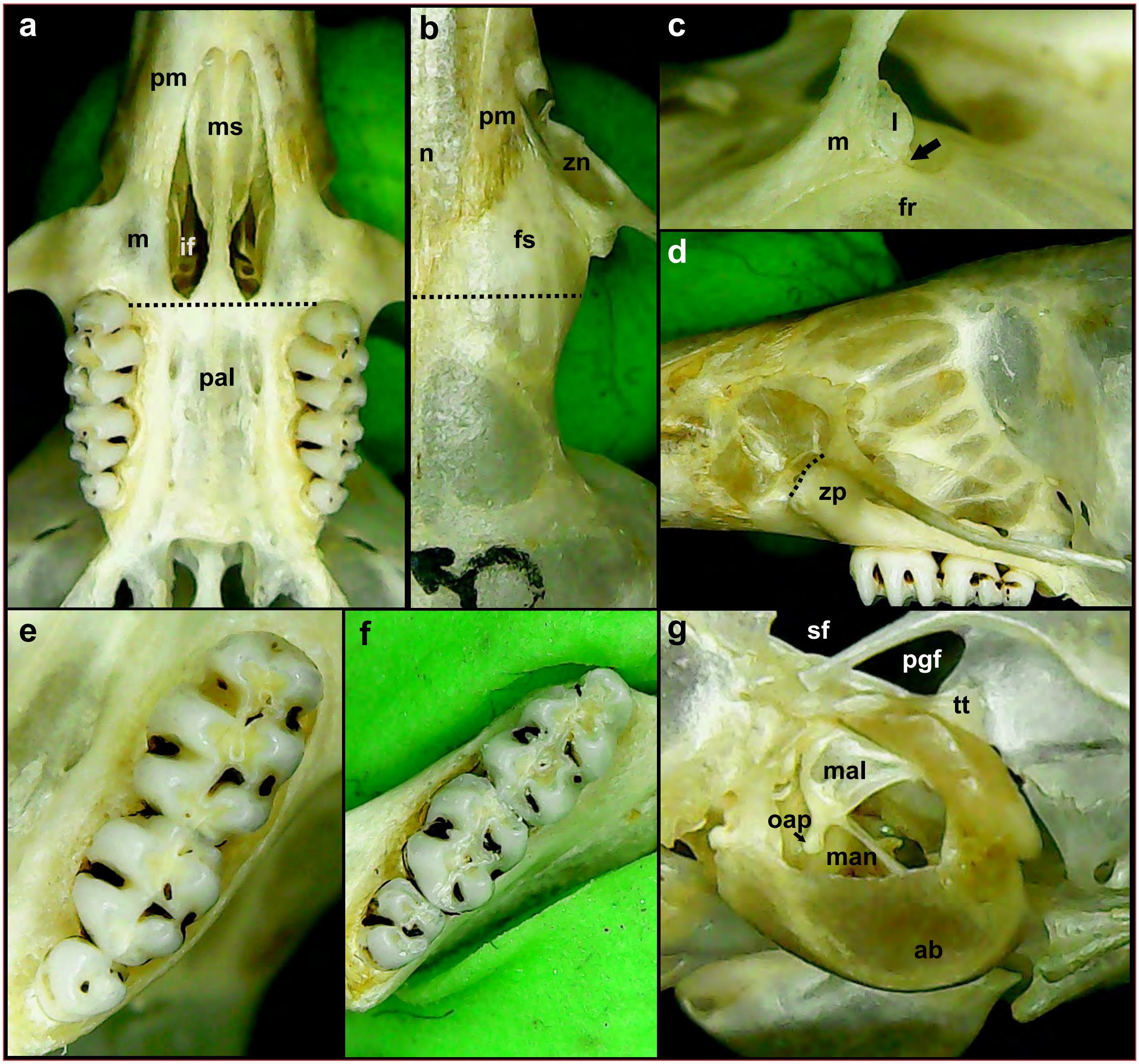
Groups classification achieved in the discriminant analysis with jackknife resampling.

	N. latebricola		***N. bogotensis***		
	Occidente	**Oriente**	**North Colombia**	**Cundinamarca**	**Total**
N. latebricola					
Occidente	11	1	1	0	13
Oriente	2	6	0	0	8
N. bogotensis					
North Colombia	0	0	1	2	3
Cundinamarca	0	0	1	0	1
Total	13	7	3	2	25

	N. latebricola		***N. bogotensis***			
	Occidente	**Oriente**	**North Colombia**	**Cundinamarca**	**Venezuela**	**Total**
N. latebricola						
Occidente	11	2	0	0	0	13
Oriente	2	6	0	0	0	8
N. bogotensis						
North Colombia	0	0	0	0	3	3
Cundinamarca	0	0	0	1	1	1
Venezuela	0	0	1	1	7	9
Total	13	8	1	1	11	34

Appendix 5

Craniodental anatomy in a specimen referred as *Neomicroxus bogotensis* (ICN13284; previously mentioned as *N. latebricola* by Ramírez-Chaves and Noguera-Urbano 2010) from Nariño department, Colombia: a, cranium in palatal view; b, right half of the cranium in dorsal view; c, lacrimal region; d, zygomatic plate region in lateral view; e, left upper molars in occlusal view; f, left lower molars in occlusal view; g, auditory region in lateral view. Abbreviations: ab: auditory bulla (ectotympanic), fr: frontal, fs: frontal sinus, if: incisive foramen, l: lacrimal, mal: malleus, man: manubrium, m: maxillary, ms: maxillary septum, n: nasal, oap: orbicular apophysis, pal: palatine, pgf: postglenoid foramen, pm: premaxillary, sf: subsquamosal fenestra, tt: tegmen tympani, zn: zygomatic notch, zp: zygomatic plate.



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Characterization of caves as bat roosts in the brazilian-paranense biogeographic region of Bolivia

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Bats play vital roles in nature as pollinators, seed dispersers, and natural controllers of insect pests. They serve as indicators of habitat disturbance and provide an insight into the health status of an ecosystem. This enormous importance contrasts with the lack of information on the current state of their roosts in Bolivia, particularly as regards caves and caverns. A search for caves and caverns was carried out in the eastern department of Santa Cruz, Bolivia, corresponding to the Brazilian-Paranense biogeographic region. Subsequently, an environmental-structural characterization of the caves was conducted to obtain biological information by capturing and identifying bats in eastern Bolivia. Interspecific associations in caves and the relationship between roost characteristics and bat diversity were explored and described based on the variables evaluated. A total of 19 caves were evaluated. A correlation between environmental and structural parameters was investigated, showing a relationship between cave length and humidity. Seven species of cave bats were identified, and two species of threatened Bolivian bats *(Lonchorhina aurita* and *Natalus macrourus*) were found in four caves. The caves evaluated are new records of this vital habitat for bats in the country. The presence or absence of bat species was found to depend on the structural characteristics of the cave (length, complexity), but not on temperature, although humidity may play a role in the presence of species. Among the species found, those highly specialized in the selection and use of roosts at caves could be prone to local extinctions. It is suggested that further investigations should be carried out on the ecology of these cave-dwelling bat species to identify the roosting patterns of bats and their distribution range, to elaborate conservation and management programs for caves and the animal communities sheltered.

Los murciélagos cumplen roles muy importantes en la naturaleza como polinizadores, dispersores de semillas, controladores naturales de plagas de insectos, son indicadores de niveles de perturbación de hábitats y ofrecen una amplia visión de la salud de un ecosistema. Esta enorme importancia contrasta con la falta de información sobre el estado actual de sus refugios en Bolivia, particularmente aquella relacionada con cuevas y cavernas. Se realizó una búsqueda de cuevas y cavernas en el este del departamento de Santa Cruz, Bolivia, correspondiente a la región biogeográfica Brasileño-Paranense. Posteriormente, se registraron las características ambientales-estructurales de las cuevas y se obtuvo información biológica mediante captura e identificación de murciélagos en el este de Bolivia. Se determinó la asociación interespecífica en las cuevas y la relación existente entre las características de los refugios con la diversidad de murciélagos con la finalidad de describir estos refugios en función a sus variables evaluadas. Un total de 19 cuevas fueron evaluadas. Los parámetros ambientales se correlacionaron con los estructurales mostrando relación entre la longitud y la humedad. Se identificaron siete especies de murciélagos cavernícolas, resaltando que en cuatro cuevas se encontraron dos especies de murciélagos amenazados (*Lonchorhina aurita* y *Natalus macrourus*) en Bolivia. Las cuevas evaluadas son nuevos registros para el país de este importante componente del hábitat. Se determinó que la presencia o ausencia de especies de murciélagos se correlaciona con las características estructurales del refugio (largo, complejidad) y no de sus valores de temperatura, aunque la humedad podría ser una causa próxima para la presencia de las especies. Se encontraron especies de alta especialización en el uso de cuevas que podrían ser susceptibles a extinciones locales. Se sugiere realizar más investigaciones sobre la ecología de estas especies de murciélagos que habitan en cuevas, a fin de identificar los patrones de refugio de murciélagos, su rango de distribución y generar programas de conservación y gestión para las cuevas y su fauna.

Keywords: caves; bats; conservation; roosts.

Introduction

Mammal recording in Bolivia has been conducted over a long time (Tarifa 2014), with the work of Sydney Anderson as a cornerstone for contemporary mammalogy in the country. Sydney Anderson conducted studies from 1964 to 1993; his efforts, which spanned over nearly three decades, resulted in a reference book for Bolivian mammalogy (Anderson 1997). In subsequent decades, the study of mammals has increased significantly, as regards not only taxonomic aspects (Aguirre *et al.* 2019) but also investigating ecological (Wallace *et al.* 2010) and conservation features (Tarifa and Aguirre 2009). Anderson was also the first to set the grounds for the study of bats in Bolivia, publishing a preliminary list of 79 species (Anderson *et al.* 1982). This information provided the basis for multiple publications on bats, including compilations of the current state of knowledge (Aguirre 2007) and taxonomic revisions (*e. g.*, Siles *et al.* 2013), up to complex ecological studies (*e. g.*, Aguirre et al. 2016; Siles *et al.* 2007). From the work of Anderson *et al.* (1982), the richness of bat species known to Bolivia has increased significantly to 138 species currently reported (Aguirre *et al.* 2019), equivalent to approximately two records of new species per year over a decade (Aguirre *et al.* 2009).

Bats, which account for some 50 % of the mammalian fauna of tropical rainforests (Patterson *et al.* 2003), play a central role as pollinators, seed dispersers, and natural pest controls in crops (Cleveland *et al.* 2006; Bracamonte 2011; Kunz *et al.* 2011). Also, they have a huge potential as indicators of habitat disturbance levels (Kunz *et al.* 2011; Castro-Luna *et al.* 2007; Park 2015) and provide a broad view of the health of ecosystems, as they exploit different trophic resources in Neotropical forests (García-Morales *et al.* 2013). This considerable importance contrasts with the lack of information on the current status of their roosts (Kunz 1982; Arita and Vargas 1995; Aguirre 2007; Siles *et al.* 2007) and the misconception or erroneous beliefs about them, leading to ungrounded extermination of individuals or colonies (Hutson *et al.* 2001; Lizarro *et al.* 2010).

Bats need roosts to shelter from adverse weather conditions and predators (Kunz and Fenton 2003), where breeding, nursing, or temporary roosting colonies are also established between migrations (Altringham 2011). Therefore, roost characteristics and roost-related processes play a central role in the ecology and evolution of different bat species (Kunz 1982).

There is little knowledge in Bolivia about the availability of roosts for bats, given the few studies carried out on this topic. Of the 138 bat species registered (Aguirre *et al.* 2019), at least 35 use caves as primary or alternative roosts (Aguirre 2007; Moya *et al.* 2007; Siles *et al.* 2007) and at least 12 can be considered as strict cave dwellers (Aguirre 2007). Bat species inhabiting these roosts may be listed under a threatened category, mainly because of the specificity of the sites uses and for having small populations, which is aggravated by the destruction or misuse of caves, indiscriminate killing, and because of negative misbeliefs and myths (Galarza and Aguirre 2007). Knowing and protecting the natural roosts of bats, especially those of threatened species, are essential for the conservation of key elements of biodiversity (Aguirre *et al.* 2010). This study aims to contribute basic information on the characteristics of cave roosts that are regularly or occasionally inhabited by bats, as well as on the use of caves (position, resting sites, and interactions), in the east of the department of Santa Cruz, Bolivia. With the data obtained, we expect to set biological bases for the implementation of conservation strategies that ensure the survival of bat populations.

Materials and Methods

Study Area. We carried out a comprehensive search of caves and caverns in the east of the department of Santa Cruz, Bolivia, corresponding to the Brazilian-Paranense biogeographic region (Navarro 2011), starting with a literature review and gathering incidental information from local inhabitants. Each of the caves was located and georeferenced in the localities (Figure 1). The localities where caves and caverns with the presence of bat species were recorded are Huanchaca Plateau, San Matías, Santiago de Chiquitos, Puerto Suárez, Roboré, Ascension de la Frontera, and San Ignacio de Velasco (Figure 1).

Characterization of caves. The fieldwork was conducted from June 2008 to March 2009, with a three-day visit to each cave. The environmental-structural characteristics of each cave were recorded using a methodology adapted from Siles *et al.* (2007). We measured the distance at both sides (width) and to the roof (height) at one-meter intervals and recorded the temperature and humidity during the same period of time in each cave (9:00 to 14:00 hrs). Since the environmental variables measured may be biased by seasonal variations, the results include the month when each cave was evaluated (Table 1), in the understanding that the data obtained characterize each cave at a particular time point. In addition, notes were made regarding the illumination in sites where individuals were recorded or the distance from the entrance to the cave.

The particular location of species within caves during the day, resting sites, and interspecific interactions were recorded on days when neither measurements were taken nor bats were captured, for a similar period of time for each cave. The size of each colony was estimated according to the number of bats observed during daytime visits: for small colonies (< 30 individuals/colony), all individuals could be counted directly; for larger colonies, photographs were taken and individuals were counted on the printout. No attempt was made to estimate absolute population sizes from catch data; instead, this information was used for validating species identification and estimating relative abundance.

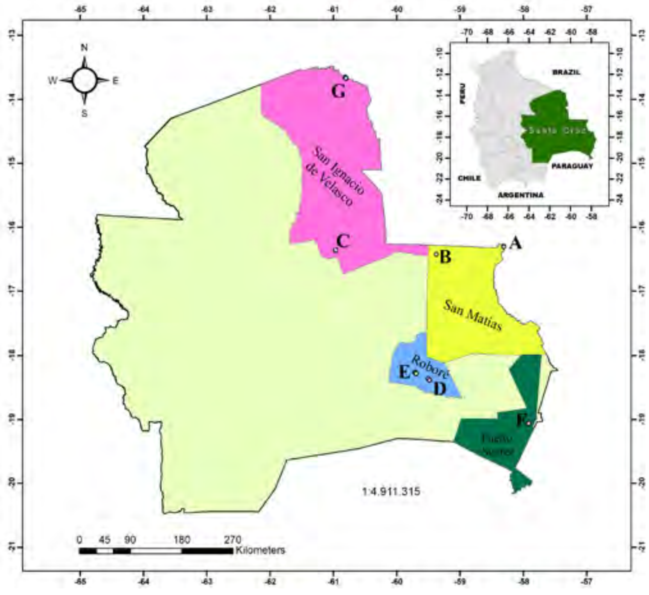

Figure 1. Location map of the 7 study sites where the 19 caves were located in the department of Santa Cruz, Bolivia. Caves are grouped according to closeness, marked with different letters (A: CU1, CU2; B: AS1; C: CY1; D: MS1, PM1, PM2; E: MN1, MN2, MN3; F: MT1; G: TR1, TR2, TR3, TG1, CR1, HJ1, TM1, TM2; see Table 1 for names).

Table 1. Summary of the environmental-structural characteristics of the 19 caves in the department of Santa Cruz, Bolivia. (Lat: Latitude, Long: Longitude, LT: Overall Length, H: Height, W: Width, Ent: Entrance, RH: Relative humidity, T: Temperature, $\bar{x}$: Average, SD: Standard Deviation, Max: Maximum, Min: Minimum).

Cave	Month	Lat.	Long.	LT (m)	H (m) (Max)	H (m) (Min)	W (m) (Max)	W (m) (Min)	N° Ent	%RH ($\bar{x}$)	%RH (SD)	%RH (Max)	%RH (Min)	T (°C) ($\bar{x}$)	T(°C) (SD)	T (°C) (Max)	T (°C) (Min)
Curicha (CU1)	June	-16.30397	-58.30754	12.0	2.5	0.8	4.4	1.5	1	68.4	1.8	70.5	64.0	26.7	0.8	27.8	26.4
Curicha 2 (CU2)	June	-16.30418	-58.30721	19.0	3.1	1.8	17.9	1.9	1	67.5	3.1	73.0	63.0	22.6	1.2	24.8	21.3
Cueva Ascensión (AS1)	June	-16.31121	-59.44959	5.0	2.8	2.5	1.5	0.6	1	71.8	5.5	79.0	66.0	24.7	2.0	26.9	21.5
Cueva del Yeso (CY1)	June	-16.35668	-60.96482	18.0	6.0	1.0	17.3	3.2	1	74.8	2.7	77.0	68.0	17.5	0.4	18.0	16.3
Miserendino (MS1)	August	-18.36037	-59.50118	208.0	40.0	1.4	7.5	0.3	3	93.8	4.8	98.0	65.0	23.9	0.9	28.5	23.0
Puente Mono 1 (PM1)	February	-18.38711	-59.48085	56.0	10.0	4.5	7.5	1.5	1	87.8	4.9	97.0	79.0	26.5	1.2	28.4	25.1
Puente Mono 2 (PM2)	February	-18.38944	-59.48050	65.0	16.0	6.5	6.0	1.0	2	86.5	3.2	94.0	83.0	26.9	0.8	27.7	24.6
Mono 1 (MN1)	August	-18.26006	-59.71580	13.0	1.9	1.4	12.0	2.5	2	52.5	6.7	61.0	45.0	32.2	4.3	37.1	28.0
Mono 2 (MN2)	August	-18.27911	-59.69929	17.0	9.5	6.0	2.5	0.4	1	57.3	2.8	61.0	52.0	25.3	0.3	25.6	24.9
Mono 3 (MN3)	August	-18.28369	-59.69608	14.0	11.0	10.5	4.5	0.3	1	53.5	1.5	56.0	52.0	26.3	0.5	26.9	25.5
Motacucito (MT1)	February	-19.05967	-57.91698	81.0	10.0	0.9	13.0	1.1	1	93.7	5.3	99.0	79.0	29.3	1.4	36.9	27.7
Torres 1 (TR1)	December	-13.66872	-60.79697	40.0	10.0	0.4	6.1	0.2	1	81.0	3.9	87.0	74.0	31.0	0.2	31.0	30.4
Torres 2 (TR2)	December	-13.66942	-60.79706	9.0	2.7	0.5	1.2	0.5	1	79.7	1.8	83.0	78.0	31.3	0.1	31.5	31.1
Torres 3 (TR3)	December	-13.66984	-60.79703	10.0	2.5	0.3	1.6	0.1	1	66.7	6.0	77.0	60.0	31.7	0.9	33.0	30.2
Tigre (TG1)	December	-13.65209	-60.81296	35.0	3.5	0.4	1.7	0.2	3	86.3	3.4	92.0	83.0	26.0	0.0	26.0	26.0
La Cruz (CR1)	December	-13.67011	-60.79615	48.0	12.0	0.5	2.0	0.3	2	87.2	3.1	94.0	79.0	26.0	0.0	26.0	26.0
Hojarasca (HJ1)	December	-13.66910	-60.79611	17.0	12.0	0.5	2.0	0.4	1	82.4	1.4	84.0	80.0	28.4	0.2	28.7	28.1
Torre Mediana (TM1)	December	-13.66678	-60.79638	10.0	7.0	0.7	2.3	0.2	1	77.2	1.6	81.0	75.0	30.4	0.2	30.7	30.2
Torre Mediana 2 (TM2)	December	-13.66706	-60.79678	9.0	9.0	1.0	1.0	0.4	1	74.8	3.1	79.0	70.0	29.4	0.4	29.8	28.8

To confirm the identity of all bat species, present in each cave, individuals were captured following the methodology by Vargas *et al.* (2006). Mist nets were placed in narrow areas of the caves to ensure the capture of bats; afterward, these individuals were identified using field keys (Emmons and Feer 1999; Aguirre *et al.* 2009) and then released.

Relationship between bat abundance and seasonality. To determine if the number of records of bat species in caves is related to the season of the year, a Chi-Square test (Zar 1999) was performed between the number of records of each species in the dry season (April to September) and the rainy season (October to March). The analysis excluded *Chrotopterus auritus* because of the small number of records for this species.

Interspecific association in caves. The association between the bat species captured in caves was analyzed using presence-absence data to calculate the interspecific association index *V* for pairs of species (Arita and Vargas 1995). Values for this index range from -1 (complete segregation), 0 (no association), to 1 (perfect positive association).

Relationship between roost characteristics and bat diversity. To characterize the caves according to the variables evaluated in roosts, a linear correlation analysis (Zar 1999) was conducted between temperature and humidity and structural variables, i.e., cave length (long), number of arms or galleries (passages of varying dimensions), number of entrances (cavities in the ceiling, on the side, or at the bottom of the cave), and structural variation (presence of structures in the roof or walls formed by the dissolution of the parental material, with cracks or cavities), in addition to the biological variables of species richness and diversity. The complexity parameters of caves were defined based on the presence of galleries, entrances, and variation (1 = Nil, 2 = Medium, 3 = Complex, 4 = Highly Complex). Accordingly, a cave with a complexity value of 1 has a single gallery, few entries (≤ 5), and no structural variation; a cave that scored 2 has two galleries, few entries (> 5, ≤ 10) and little variation in the structure of the roof; a cave that scored 3 has three galleries, entrances (> 10, ≤ 20) and little variation in the roof and walls; a cave that scored 4 has more than three galleries, entrances (> 20) and a great variation in roof and walls. The relationship of environmental and structural variables with species was explored with a Canonical Correspondence Analysis (CCA), including a permutation test to evaluate the significance of the variables in the analysis (Tel-Braak 1986). The statistical analyses used in the present work were carried out with the program R (v. 3.2.2).

Results

Seven localities were visited during the study period, finding 19 caves that were georeferenced (Figure 1). Of these, 12 were identified for the first time and named according to their particular characteristics or locations. The mean temperature and humidity, as well as the structural features of each cave, are described in Table 1.

As regards the species composition of roosting bats, we recorded the presence of seven species in three families: Phyllostomidae (4), Natalidae (1), and Emballonuridae (2). The family Phyllostomidae was represented by four subfamilies: Carolliinae, Desmodontinae, Lonchorhininae, and Phyllostominae. The species recorded (ranked from higher to lower frequency of occurrence in caves, in parenthesis) were *Peropteryx macrotis* (12 caves), *Carollia perspicillata* (7), *Desmodus rotundus* and *Natalus macrourus* (3), *Peropteryx kappleri* (2), and *Chrotopterus auritus* and *Lonchorhina aurita* (1; Figure 2).

The observed abundance data are summarized in Table 2, showing that cave MT1 had the highest abundance for three species (*C. perspicillata*, *D. rotundus,* and *N. macrourus*). Two individuals of *C. auritus* and eight of *L. aurita* were found in cave CU1. Caves AS1 and MN1 showed the smallest number of individuals ($n = 5$) in both caves, with a single species (*P. macrotis*). On the other hand, cave HJ1 attained the highest number of individuals of *P. macrotis*. It should be mentioned that no individuals were found in cave PM2.

There was a significant relationship between the number of species records in caves and the time of year (Pearson's Chi-square = 72.4; d.f. = 5; $P = 0.01$). In general, we recorded more individuals in caves during the wet season, although the proportions vary according to the species.

As regards interspecific associations in caves, we calculated the *V* index for all potential pairs of the seven species found in caves, for a total of 21 combinations. This resulted in 12 cases of negative interspecific association; of these, none showed an absolute value of -1, i.e., the species involved are not completely segregated. There was no case where with *a V* value of zero (i.e., no association). On the other hand, we found nine cases of a positive association, with a *V* value of 1 (perfect positive association) only in three cases, namely *L. aurita-C. perspicillata*, *L. aurita-C. auritus*, and *C. auritus-C. perspicillata* (Table 3).

Table 2. Total abundance of bat colonies in caves, as calculated by direct daytime observations and photographs. *Cper = C. perspicillata, Drot = D. rotundus, Caur = C. auritus, Laur = L. aurita, Nmac = N. macrourus, Pmac = P. macrotis, Pkap = P. kappleri.*

Caves	*Cpe*	*Dro*	*Cau*	*Lau*	*Nma*	*Pma*	*Pka*	Total
Curicha (CU1)	12	5	2	8	0	0	0	27
Curicha 2 (CU2)	15	10	0	0	6	0	0	31
Cueva Ascensión (AS1)	0	0	0	0	0	5	0	5
Cueva del Yeso (CY1)	15	0	0	0	0	0	0	15
Miserendino (MS1)	0	0	0	0	25	0	0	25
Puente Mono 1 (PM1)	0	0	0	0	0	8	0	8
Puente Mono 2 (PM2)	0	0	0	0	0	0	0	0
Mono 1 (MN1)	0	0	0	0	0	5	0	5
Mono 2 (MN2)	0	0	0	0	0	8	0	8
Mono 3 (MN3)	0	0	0	0	0	22	0	22
Motacucito (MT1)	35	50	0	0	10	0	0	95
Torres 1 (TR1)	10	0	0	0	0	25	0	35
Torres 2 (TR2)	0	0	0	0	0	10	0	10
Torres 3 (TR3)	0	0	0	0	0	15	14	29
Tigre (TG1)	7	0	0	0	0	4	0	11
La Cruz (CR1)	19	0	0	0	0	0	12	31
Hojarasca (HJ1)	0	0	0	0	0	31	0	31
Torre Mediana (TM1)	0	0	0	0	0	20	0	20
Torre Mediana 2 (TM2)	0	0	0	0	0	11	0	11
Total	113	65	2	8	41	164	26	419

The assessments of caves revealed that the colonies of *P. macrotis* were compact groups, in contact with each individual, and separated from all other species. We also observed that *D. rotundus* roosts in hard-to-access areas of the cave but can coexist in the proximity of individuals of *C. perspicillata*, *L. aurita*, *C. auritus*, and *N. macrourus*.

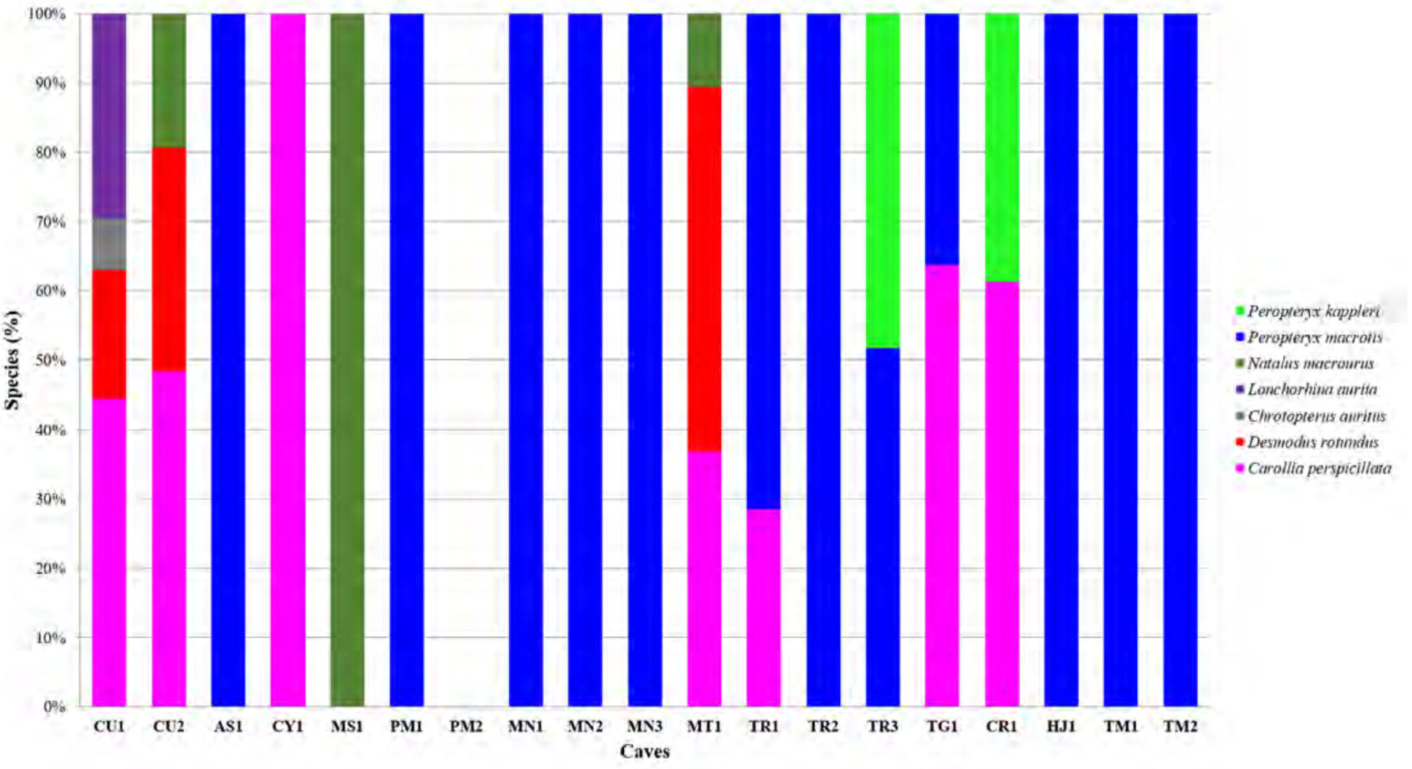

Figure 2. Bat species present in the caves evaluated in the eastern portion of the department of Santa Cruz, Bolivia. Percentages represent the relative abundance of species.

Table 3. Association index values (*V*) calculated for pairs of species present in the caves of the department of Santa Cruz, Bolivia.

Species	Cpe	Dro	Cau	Lau	Nma	Pma	Pka
P. kappleri (*Pka*)	0.1	-0.1	-0.1	-0.1	-0.1	-0.1	
P. macrotis (*Pma*)	-0.5	-0.6	-0.3	-0.3	-0.6		
N. macrourus (*Nma*)	0.3	0.6	-0.1	-0.1			
L. aurita (*Lau*)	1.0	0.5	1.0				
C. auritus (*Cau*)	1.0	0.5					
D. rotundus (*Dro*)	0.6						
C. perspicillata (*Cpe*)							

The linear correlation analysis (Table 4) shows that long caves are characterized by higher HR; this environmental parameter is related to the structural complexity of the cave. Similarly, caves with a complex structure show a relationship with the number of galleries.

According to the Canonical Correspondence Analysis (Figure 3), the first two axes explain 22 % of the variation in the data. This analysis shows that *C. perspicillata* prefers complex caves with more galleries (MT1 and CR1); *N. macrourus* prefers structurally long caves with high RH (MS1 and MT1); *P. macrotis* is found in simple caves that record high temperatures (average 28.6 °C); and *D. rotundus* prefers structurally long caves with high RH.

Discussion

Caves are vital resources allowing the existence of species that are key for ecosystems, such as bats (Altringham 2011). This contrasts with the scarce information on cave bat roosts in Bolivia, given the few studies conducted in this country to date. Thus, to date, only four speleological zones had been recorded for the country: Sorata (La Paz), Carrasco National Park (Cochabamba), Torotoro (Potosí), and Puerto Suárez (Santa Cruz), all including caves that harbor bat species (Aguirre 2007; Miranda-Chumacero 2007). Therefore, the 19 caves identified in the present study are an important contribution to the knowledge of cave roosts in Bolivia, with different species of bats found in 95 % of these shelters.

Regarding the abundance of bats in caves, Arita (1996) mentions that the largest caves shelter the highest numbers of individuals. However, it should be noted that cave size is also related to structural complexity, as larger caves tend to have more chambers, tunnels, and bifurcations. Sherwin *et al.* (2000) show that simple caves are less populated by bats than those of greater complexity, while Siles *et al.* (2007) report that caves with high structural complexity tend to shelter a higher abundance of bats than less complex caves of similar size. In our case, cave MT1 follows the same trend: it has the most complex structure, which is probably the reason for the higher abundance of bat species that make good use of the various structural areas to roost.

Some species appear to prefer particular structures in caves. For example, *D. rotundus* roosted in darker and narrower cavities, consistent with the observation reported in this same species by Siles *et al.* (2007). The use of deeper chambers in caves by compact groups of bats has been reported for *Artibeus jamaicensis* (Arita and Vargas 1995; Ortega and Arita 1999), *C. perspicillata* (Trajano and Gimenez 1998; Reis *et al.* 2007), *Phyllostomus hastatus* (McCracken and Bradbury 1981), *Pteronotus parnellii* and *Diphylla ecaudata* (Arita and Vargas 1995). In the present study, this pattern was observed for *C. perspicillata*, forming compact groups at the bottom of all caves where it was found. Similarly, our data indicate that *N. macrourus* prefers to roost in caves with very high humidity, since the colonies of this species were always located in narrow passages of low height. This same characteristic was observed by Torres-Flores and López-Wilchis (2010) in *Natalus stramineus* roosting in different caves of Mexico.

One of the major drivers for the presence of bats in caves is microclimate (Kunz 1982), which depends on the length, number of entrances, and depth of the cave, as well as on the temperature and humidity inside it

Table 4. Correlation matrix between the variables studied. Bottom: Correlation values (r) between variables, Top: Significance values of the correlation values. (Shaded values show significant correlations at 95 % confidence, α < 0.05).

	RH	Temp.	Lenght	Arms	Entrance	Complexity	Diversity	Richness
RH		0.650	0.006	0.414	0.126	0.051	0.911	0.990
Temp.	-0.112		0.398	0.790	0.576	0.921	0.990	0.962
Lenght	0.602	-0.206		0.579	0.540	0.453	0.796	0.986
Arms	0.199	0.066	-0.136		0.014	0.001	0.607	0.473
Entrance	0.364	-0.137	0.150	0.554		0.128	0.902	0.624
Complexity	0.454	-0.024	0.183	0.715	0.362		0.027	0.016
Diversity	0.027	-0.003	0.064	0.126	-0.030	0.508		0.000
Richness	-0.003	-0.012	0.004	0.175	-0.120	0.546	0.957	

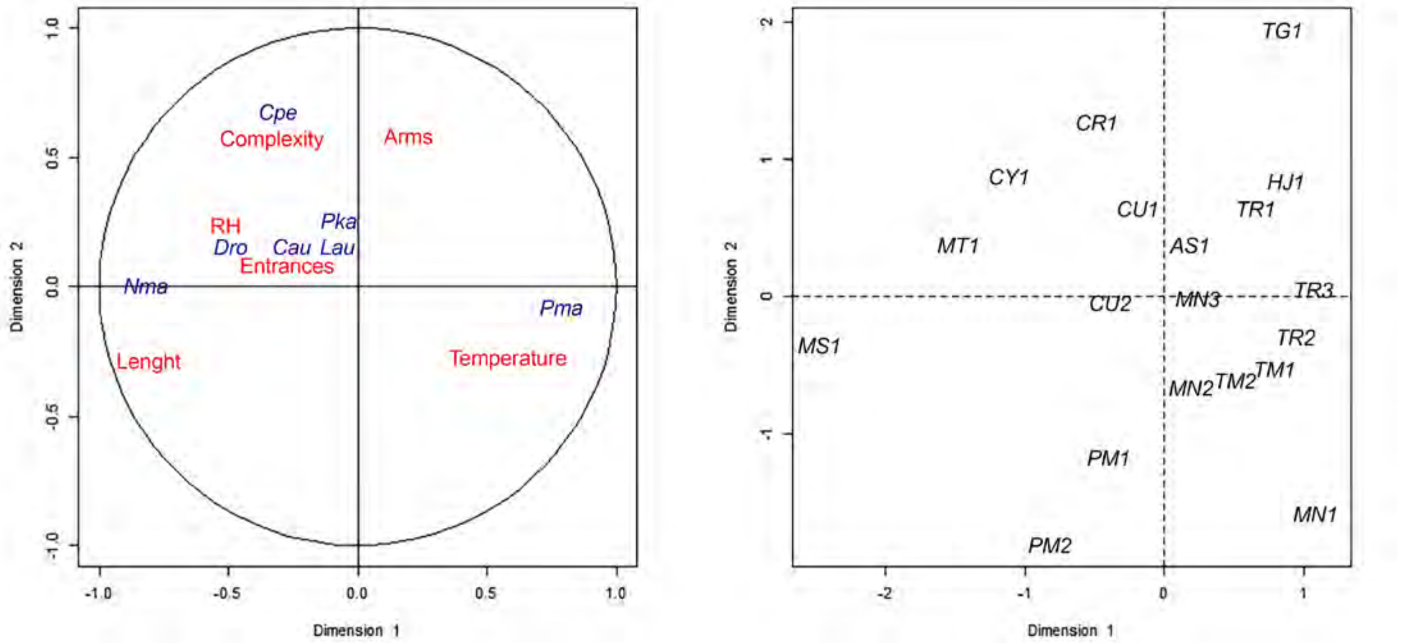

Figure 3. CCA of bat species and environmental-structural characteristics of the caves evaluated. Abbreviations represent each of the caves and bat species evaluated (Cpe: *C. perspicillata*, Dro: *D. rotundus*, Cau: *C. auritus*, Lau: *L. aurita*, Nma: *N. macrourus*, Pka: *P. kappleri*, Pma: *P. macrotis*).

(Siles *et al.* 2007). The temperature and humidity records showed differences between the 19 caves evaluated. The roosts with the greatest variations in temperature and relative humidity inside caves were MN1, TR3, AS1, MT1, PM1, and MS1 (Table 1), likely as a result of their structural complexity. These features probably provide bats with habitat conditions that best suit their metabolic or energy requirements (Lewis 1995; Sedgeley and O'Donnell 1999). Siles *et al.* (2007) detected no relationship between temperature and species composition across caves. In the 19 caves explored, bat species probably choose roosting sites based on structural rather than environmental characteristics, although both features (i.e., structure and microclimate) should not be separated, as they are often related (Lewis 1995). Nonetheless, it is challenging to derive generalizations with these data, as temperature was recorded only once in each cave; thus, it should not be used as an indicator of the microclimate inside a cave. Thus, we recommend recording continuous readings over long periods of time (Sherwin *et al.* 2000). Therefore, continuous monitoring of these caves should be conducted to accurately determine the role of this abiotic factor on the presence and abundance of bats.

On the other hand, the calculated *V* index values may not show the existence of a particular interspecific interaction, since the fact that two species co-occur in the same roost (cave) does not necessarily imply that both are positively associated. An improved analysis of interspecific associations in caves should consider whether pairs of species occupy the same area within roosting caves. Caves offer a wide variety of sites for bat species to choose from (Hill and Smith 1992; Altringham 1996). Our study evidenced the segregation of some species within their roosts (*e. g.*, *P. macrotis* and *P. kappleri*), which remain clearly separated from all other bat species in the caves where they were recorded. Therefore, we agree with Swift and Acey (1983), who indicate a nonexistent interspecific interaction when a pair of species occupying the same roosting cave use separate areas within it, leaving and arriving at different times, foraging in different areas, and feeding on different preys. Also, in this study, it was observed that *D. rotundus* shelters in hard-to-access sectors of the cave but might occupy perch sites close to individuals of *C. perspicillata*. These observations are consistent with those reported by Siles *et al.* (2007), who mention that no interaction between these two species was observed. All our combinations between *L. aurita*, *C. perspicillata*, and *C. auritus* showed a positive association. However, it should be noted that very few individuals were observed or captured; moreover, only these three species co-occur within a single cave. Graham (1988) pointed out that cases where pairs of species roost in the same site are exceptional, being the only ones that clearly showed positive associations between species.

The analysis of the conservation status of bats in Bolivia shows that, of the 138 species present in the country, 12 face some risk level. In the present study, we found *L. aurita* and *N. macrourus*, which inhabit cave environments only (Lassieur and Wilson 1989; Emmons and Feer 1999) and are categorized as "Endangered" and "Vulnerable", respectively (Vargas and Rocha 2009; Vargas *et al.* 2009). The records of both species in this study are relevant from a conservation standpoint. *L. aurita* is a species distributed from Mexico to southeastern Bolivia (Vargas *et al.* 2009) that may potentially live in mountain ranges in the Chiquitano and Cerrado forest ecoregions and areas adjacent to wetlands (Vargas *et al.* 2010). To date, the cave reported in San Matías is the only known in Bolivia where this species is present. For *N. macrourus*, the records confirm its presence in caves MT1 and MS1, as previous reports involving these caves came from personal observations (Aguirre 2007;

Vargas 2008). Thus, the cave CU2 is a new record of a cave inhabited by this species, considering that only confirmed reports about the distribution of this species in Brazil were available (Delgado-Jaramillo *et al.* 2018). In this way, caves can constitute important shelters for these species classified as threatened in Bolivia (Aguirre *et al.* 2010).

Most of the 19 caves evaluated in Santa Cruz represent new records of this type of important environments for bats in Bolivia and thus serve as references for advancing the knowledge about natural history and as key tools for future research on cave ecology.

In this work, we found bat species that could be susceptible to local extinctions, given their highly specialized use of caves. Because of the importance of new bat records in caves, we suggest that the entities involved should manage the conservation of the sites mentioned, in addition to coordinating actions to establish a system of protected areas called Areas or Sites Important for the Conservation of Bats (AICOMs/SICOMs).

This work aims to contribute solid elements to advance the knowledge of cave bat species and their roosting requirements, laying the grounds for future research. Caves are sources of valuable information on population structure, reproduction, behavior, and interspecific association of bat species; in addition, the information in this study contributes to identify shelters requiring conservation measures in our country.

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Home range of the mouse *Phyllotis osilae* in forest fragments of *Polylepis subtusalbida* with different habitat matrix

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Home range is an aspect of ecology that allows us to understand the mechanisms and spatial relationships that underlie habitat choice and animal responses to environmental change. However, studies on this subject have been focused mainly on medium and large mammals, while those on small mammals are scarce. Small mammals play important roles in maintaining ecological processes, such as the survival of several plant species. *Phyllotis osilae* is a phyllotine rodent, which functions as a potential seed disperser for *Polylepis subtusalbida*, a tree that is endemic and categorized as Vulnerable (VU) for Bolivia. The forests of *P. subtusalbida* are highly fragmented, with reforestation with introduced species such as *Pinus radiata* and *Eucalyptus globulus*. The question we pose for this study is: how does the home range of *P. osilae* vary between fragments of *P. subtusalbida* with different types of matrix (natural grassland and exotic tree plantations)? The study was carried out on four fragments of *P. subtusalbida* in Tunari National Park in the city of Cochabamba, Bolivia: two fragments in the exotic tree plantation matrix (Pajcha locality) and two in the natural grassland matrix (San Miguel locality). For telemetry purposes, radio collars were installed on 16 individuals. The home ranges were calculated using the Minimun Convex Polygon (MCP) at 95 %, in the same way the Kernel density (KDE) was estimated at 95 %. The percentage of presence of *P. subtusalbida* and matrix trees within each home range was determined, with an area interval between 50.5 m^2 and 3,010 m^2. No significant differences were found between both matrices regard to the area of activity; however, in the comparison of the percentages of presence of *P. subtusalbida* trees and matrix, significant differences were found. Our results for home ranges show that the matrix would not have an effect on the area, but on its mobility; this is evidenced by the absence of movements of *P. osilae* from the fragments to the exotic matrix. In this case, the exotic tree matrix is operating as a barrier and is reflected in the almost total absence of this vegetation matrix in the home range. *P. osilae* may be playing an important role in the recovery and conservation of these ecosystems, so knowing aspects of their natural history as well as their responses to fragmentation is of great importance in understanding the fate of the *Polylepis* forests.

El ámbito hogareño es un aspecto de la ecología que permite comprender los mecanismos y las relaciones espaciales que fundamentan la elección del hábitat y las respuestas de los animales a los cambios ambientales. Sin embargo, los estudios de esta temática han sido enfocados principalmente a mamíferos medianos y grandes, en contraste los de pequeños mamíferos son escasos. Los pequeños mamíferos cumplen roles importantes para el mantenimiento de procesos ecológicos, como la sobrevivencia de varias especies de plantas. *Phyllotis osilae* es un roedor filotino, que funciona como potencial dispersor de semillas de *Polylepis subtusalbida*, un árbol endémico y categorizado como Vulnerable (VU) para Bolivia. Los bosques de *P. subtusalbida* están altamente fragmentados, presentando entre sus principales amenazas la reforestación con especies introducidas como *Pinus radiata* y *Eucalyptus globulus*. La pregunta que planteamos para este estudio es ¿cómo varía el ámbito hogareño de *P. osilae* entre fragmentos de *P. subtusalbida* con diferente tipo de matriz (pastizal natural y plantaciones de árboles exóticos)? El estudio se realizó en cuatro fragmentos de *P. subtusalbida* en el Parque Nacional Tunari de la ciudad de Cochabamba, Bolivia: dos fragmentos en la matriz de plantaciones de árboles exóticos y dos en la matriz natural de pastizal. Para la telemetría se instalaron radio collares a 16 roedores. Los ámbitos hogareños se calcularon mediante el *Minimun Convex Polygon* (MCP) al 95 %, del mismo modo se estimó la densidad de Kernel (KDE) al 95 %. Se determinó el porcentaje de presencia de árboles de *P. subtusalbida* y matriz dentro de cada ámbito hogareño, con un intervalo de área entre 50.5 m^2 a 3,010 m^2. No se encontraron diferencias significativas entre ambas matrices respecto a el área de actividad; sin embargo, en la comparación de los porcentajes de presencia de árboles de *P. subtusalbida* y matriz, si se encontraron diferencias significativas. Nuestros resultados muestran que la matriz no tendría un efecto sobre el área, pero si sobre su movilidad. Esto se evidencia en la ausencia de movimientos de *P. osilae* de los fragmentos a la matriz exótica. En este caso, la matriz de árboles exóticos está operando como una barrera y se ve reflejado en la ausencia casi total de matriz de esta vegetación en el ámbito hogareño. *P. osilae* puede estar cumpliendo un rol importante en la recuperación y conservación de estos ecosistemas, por lo que conocer aspectos de su historia natural al igual que conocer sus respuestas a la fragmentación es de mucha importancia para comprender el destino de los bosques de *Polylepis*.

Keywords: endemic; fragmentation; *Polylepis*; telemetry.

Introducción

El ámbito hogareño es el área utilizada por un individuo para buscar alimento, reproducirse, descansar y realizar todas sus actividades diarias (Burt 1943). Además, es un aspecto de la ecología que proporciona respuestas a muchas preguntas biológicas relacionadas con la dinámica de la población, las interacciones sociales, patrones de espaciamiento (Eiris y Barreto 2009) y distancia de dispersión (Santini *et al.* 2013). El análisis del ámbito hogareño es un primer paso importante para comprender los mecanismos y las relaciones espaciales que fundamentan la elección del hábitat y las respuestas de los animales a los cambios ambientales (Cumming y Cornélis 2012). Asimismo, el ámbito hogareño de hembras y machos pueden explicar distintos efectos del medio ambiente, debido a que en las hembras están relacionado con la distribución espacial de recursos y cobertura (Bonatto *et al.* 2012), mientras que para los machos dependen de la distribución espacial de las hembras (Ostfeld 1985). A la fecha, se carece de información sobre el ámbito hogareño para muchas especies o hábitats particulares (Wood *et al.* 2010). Tradicionalmente, los estudios de ámbito hogareño han sido enfocados principalmente a mamíferos medianos y grandes, y es muy difícil encontrarlos en pequeños mamíferos (Harris *et al.* 1990; Dressler *et al.* 2016).

Los pequeños mamíferos cumplen roles de importancia vital para el mantenimiento de procesos ecológicos, como la sobrevivencia de varias especies de plantas, la cual depende de la interacción de planta-animal que tiene efectos en la dispersión desde la planta madre, escarificación y enterramiento de las semillas (Tarifa y Aguirre 2009). Los roedores filotinos (Phyllotini Vorontsov, 1959) son pequeños mamíferos comunes en bosques de *Polylepis* (Yensen y Tarifa 2002). En este estudio, nos enfocamos en *Phyllotis osilae*, un roedor abundante en bosques *Polylepis subtusalbida* (Vargas *et al.* 2007; Tarifa y Yensen 2001) y a la vez un consumidor de semillas de esta especie (Balderrama 2013, com. pers.), por lo que su presencia y consumo de semillas de *Polylepis* lo hace un potencial dispersor.

Los bosques de *Polylepis* (Rosaceae, Sanguisorbeae) son bosques nativos altamente fragmentados a lo largo de su distribución; en Bolivia se ha estimado que ocupan el 10 % de su distribución original (Fjeldså y Kessler 2004). *Polylepis subtusalbida* es una especie endémica para Bolivia y, según los criterios de la IUCN (Arrázola 2011) aplicados a la flora amenazada de Bolivia, está categorizado como Vulnerable (VU; Ministerio de Medio Ambiente, Agua y Cambio Climático 2011). Entre sus principales amenazas está la reforestación con especies introducidas como *Pinus radiata* y *Eucalyptus globulus* (Arrázola 2011). Estos árboles exóticos son parte ahora del estrato arbóreo donde están presentes los bosques de *P. subtusalbida* (Gareca *et al.* 2007), formando la matriz del paisaje de estos bosques fragmentados. En la ecología del paisaje, el modelo parche-corredor-matriz define a la matriz como el tipo de elemento dominante, más extensa y coherente del paisaje (Forman 1995). El tipo de matriz que rodea los hábitats fragmentados tienen efectos significativos sobre la biodiversidad en diferentes tipos de paisaje, escalas espaciales, enfoques ecológicos y grupos taxonómicos (Prevedello y Viera 2010). Los pequeños mamíferos que dependen del bosque, pero persisten en paisajes fragmentados, pueden ser utilizados como modelos para cuantificar los efectos de la pérdida y fragmentación del hábitat, y guiar las acciones de conservación para mejorar el bienestar de los animales en paisajes fragmentados (Delciellos *et al.* 2018).

Los mamíferos de los bosques de *Polylepis* han recibido poca atención científica (Yensen y Tarifa 2002) y la distribución de los animales asociados a estos bosques ha sido poco estudiada (Fjeldså y Kessler 2004). La falta de conocimiento sobre las especies de mamíferos en los bosques hace imposible comprender su historia natural, ecología y estado de conservación, siendo un hábitat altamente amenazado y fragmentado (Tarifa y Yensen 2001). Conocer las respuestas a la fragmentación de estos bosques nativos es esencial tanto para predecir su propio destino como para comprender el destino de los árboles que dependen de ellos (Jorge 2008). Por esta razón se evalúa la variación del ámbito hogareño de *P. osilae* entre fragmentos de *P. subtusalbida* con el pastizal natural y las plantaciones de árboles de *Pinus radiata* y *Eucalyptus globulus.*

Material y métodos

El estudio se realizó en cuatro fragmentos de *P. subtusalbida* en el Parque Nacional Tunari de la ciudad de Cochabamba, Bolivia (Figura 1): dos fragmentos se encuentran en la localidad de Pajcha con superficies de 10.7 ha y 3.6 ha (17°19'22.02"S 66°8'12.15"W; 17°19'39.72"S 66°7'58.26"W) con una matriz de plantaciones de árboles exóticos compuesto por *Pinus radiata* y *Eucalyptus globulus*; dos fragmentos se encuentran en la localidad de San Miguel con superficies de 5.1 ha y 12.1 ha (17°16'36.68"S. 66°19'46.50'W; 17°16'27.30"S. 66°20'13.25"W) con una matriz natural de pastizales compuestos por *Calamagrostis* sp., *Cheilanthes pruinata, Cyperus* sp., *Eryngium paniculatum, Festuca dolichophylla, Gamochaeta* sp., *Gnaphalium dombeyanum, Lupinus* sp., *Luzula* sp., *Puya tunariensis, Stevia samaipatensis* y *Stipa ichu*. Ambas localidades se encuentran dentro el piso ecológico altimontano distribuidos en las laderas montañosas meridionales medias de la Cordillera del Tunari. La vegetación potencial natural del piso altimontano es dominado por *P. subtusalbida*, en los meses de mayo a agosto se presenta la época de sequía que coincide con el tiempo más frio (-3 y -6 °C, respectivamente). De diciembre a febrero se presenta la época de lluvias que coincide con el tiempo cálido y se presentan precipitaciones anuales de 45 a 60 % (Navarro *et al.* 2015).

El trabajo se realizó durante los meses de marzo a junio del 2013, terminando la época de lluvias y comenzando la época de sequia. Para la captura de *P. osilae*, se instalaron 160 trampas tipo Sherman para pequeños mamíferos en cada fragmento, siguiendo un protocolo de muestreo en micromamíferos altoandinos (Ruiz *et al.* 2004). Se realizaron líneas de trampeo, cada línea con 10 trampas y una separación de 10 m. Se instalaron cinco líneas paralelas a los bordes, una al centro y dos a ambos lados del borde hasta una distancia de 20 m al interior del fragmento y la matriz. Las líneas de trampeo estuvieron activas de una a tres noches, sumando un esfuerzo de 480 trampas por fragmento. Como cebo se utilizó avena, esencia de vainilla, mantequilla de maní y uvas pasa. La revisión de las trampas y recebado se realizó cada 12 h. Una vez capturados los individuos necesarios para la realizar la telemetría se procedió a cerrar las líneas, para evitar recapturarlos.

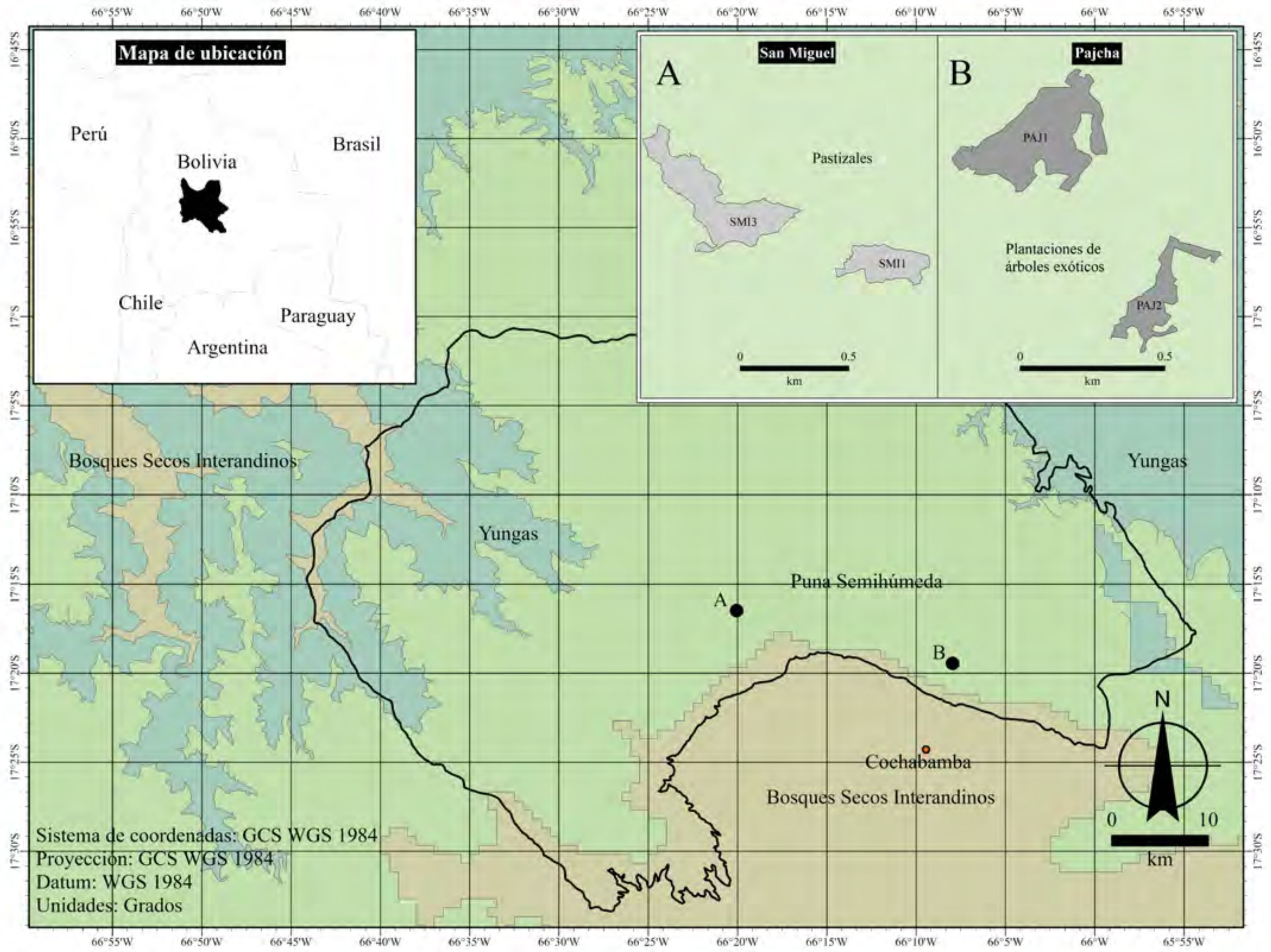

Figura 1. Mapa del área de estudio. Limites del Parque Nacional Tunari y subecoregiones presentes (Ibisch y Mérida 2003). Las ubicaciones de los fragmentos de *Polylepis subtusalbida* se indican con letras. A): Localidad de San Miguel con una matriz de pastizales, fragmentos SM13 y SM11. B): Localidad de Pajcha con una matriz de plantaciones de árboles exóticos compuesto por *Pinus radiata* y *Eucalyptus globulus*, fragmentos PAJ1 y PAJ2.

Para el manejo y manipulación de los individuos capturados se siguieron los lineamientos propuestos por Sikes *et al.* (2016), en concordancia con las leyes nacionales del Estado Plurinacional de Bolivia (Autorización MMAyA-VMA-DGBAP N° 619/12). Los roedores se identificaron mediante claves (Hershkovitz 1962; Steppan 1995; Anderson 1997; Spotorno *et al.* 2004; Jayat y Pacheco 2006) y se registraron medidas morfométricas convencionales: longitud total, cola, pata posterior, oreja (Anderson 1997), también se registró el sexo, estado reproductivo, código numérico de los individuos, fragmentos de la matriz en donde se ubicaron sus ámbitos hogareños y el peso. El pesado de los individuos se obtuvo con una pesola de capacidad de 100 g y precisión de ± 0.3 %; la exactitud del peso de los individuos fue un factor determinante para la instalación de los transmisores.

Para la telemetría se instalaron radio collares VHF Telenax (TXB-004G) solamente a individuos en los que el peso del transmisor no superó en 5 a 10 % el peso del animal (Sikes *et al.* 2011); para la instalación se siguieron las consideraciones y recomendaciones de White y Garrot (1990). El seguimiento de telemetría se realizó por nueve días en promedio, debido a la duración de la batería del transmisor, desde las 19:00 a 3:00 por los hábitos nocturnos que presenta *P. osilae*. El seguimiento no incluyó las primeras 24 horas tras liberar a los individuos, para permitir que se acostumbraran a los transmisores. Para el seguimiento se usó un receptor Telonics (TR-4K) y una antena Yagi de tres elementos, la posición se determinó mediante triangulación con un lapso de 60 minutos (en promedio) entre cada posición. Para cada posición se registraron sus coordenadas geográficas (punto fijo o *fixed point*). Se registraron datos adicionales de distancia y azimut entre cada punto fijo. Los ámbitos hogareños se calcularon en el programa BIOTAS Versión 2.0 Alpha (Ecological Software Solutions LLC) mediante el Polígono Mínimo Convexo (*Minimun Convex Polygon*, MCP) al 95 % (Mohr 1947), también se estimó la densidad de Kernel (KDE; Worton 1989) al 95 % para facilitar comparaciones.

Se determinó el porcentaje de presencia de árboles de *P. subtusalbida* y matriz dentro de cada ámbito hogareño de pastizal natural y plantaciones de *P. radiata* y *E. globulus* se sobrepuso una cuadricula sobre el área de actividad. Se utilizó una imagen satelital WorldView-2 (resolución espacial 0.5 m) para la localidad de Pajcha y para la localidad de San Miguel una imagen satelital Maxar Technologies (resolución espacial 30 m). En ambas imágenes satelitales fue posible identificar árboles de *P. subtusalbida* y la matriz. La fotointerpretación se realizó con los softwares de ArcGIS 10.2 (Esri, USA) y Google Earth Pro (Google LLC, USA). Se compararon las estimaciones de los ámbitos hogareños con el tamaño de muestra mediante una regresión lineal, con el software PAST Versión 4.03 (Hammer 2001), para determinar la independencia de las estimaciones. Se realizó un ANCOVA para comprobar las diferencias entre localidades para el área del ámbito hogareño y una prueba de U de Mann-Withney para los porcentajes de presencia (árboles de *Polylepis* y matriz), ambos estadísticos fueron calculados mediante el software PAST Versión 4.03 (Hammer 2001).

Resultados

Capturamos tres especies de roedores para ambas localidades: *Akodon boliviensis*, *Oxymycterus paramensis* y *Phyllotis osilae*. Se monitoreó un total de 16 individuos de *P. osilae*, siete hembras y un macho en la localidad de Pajcha (matriz de árboles exóticos), y cinco hembras y tres machos en la localidad de San Miguel (matriz natural de pastizales). Las comparaciones entre las estimaciones de los ámbitos hogareños con el tamaño de muestra indica que no hay independencia (r = 0.775, t = 4.5956, *P* = 0.0004). Se estimó el área y perímetro de los ámbitos hogareños (Tabla 1; Figuras 2, 3), donde se obtuvo 3,010 m^2 como el área máxima para la hembra H2 (Figura 3) y una mínima de 50.5 m^2 para la hembra H5 (Figura 4). El área y perímetro núcleo (Kernel 95 %) no se obtuvo para todos los individuos debido al número limitado de puntos fijos. En promedio, se tuvieron nueve noches consecutivas de seguimiento, a excepción del macho M8, que después del tercer día se perdió la señal del transmisor (Tabla 1).

Dentro del área de los ámbitos hogareños de *P. osilae* se obtuvieron los porcentajes de presencia de árboles de *P. subtusalbida,* y matriz (árboles exóticos y pastizal natural; Figura 4). En la localidad de Pajcha se observó que, en su mayoría, los individuos presentaron un mayor porcentaje de árboles de *P. subtusalbida* (Figura 2). En contraste, en la localidad de San Miguel la presencia tanto de árboles de *P. subtusalbida* como de matriz natural de pastizal fue similar (Figura 3), e incluso se obtuvo el registro de la hembra H10 (Figura 3) que presentó un 80 % de matriz natural de pastizales dentro su ámbito hogareño.

En las comparaciones de área del ámbito hogareño entre las localidades de Pajcha y San Miguel no se encontraron diferencias significativas (F = 0.078, d. f. = 1, *P* = 0.784). Sin embargo, sí se encontraron diferencias significativas al comparar el porcentaje de presencia de árboles de *P. subtusalbida* y la matriz (W = 0.5, p = 0.0006639).

Discusión

Los efectos de especies forestales introducidas en los bosques nativos de *P. subtusalbida* han sido estudiados en los últimos años (Aguirre *et al.* 2004; Martínez *et al.* 2006; Aguirre *et al.* 2007; Gareca *et al.* 2007; Solís *et al.* 2014). Gareca y Martínez (2015) encontraron que las especies introducidas afectan en la reproducción y regeneración de *P. subtusalbida*, y este efecto

Tabla 1. Áreas y perímetros de los ámbitos hogareños de *Phyllotis osilae*. Hembra (H), macho (M).

Código	N. fixed points	N. noches	Área (m^2) MCP 95 %	Perímetro (m) MCP 95 %	Área (m^2) Kernel 95 %	Perímetro (m) Kernel 95 %
			Localida de Pajcha			
H1	46	10	1,035.5	140.58	1,068.72	270.61
H2	63	10	3,010	207.70	2,271.65	426.41
H3	35	10	1,502	155.78	-	-
H4	45	10	1,491	156.18	1,777.89	297.11
H5	19	9	50.5	34.27	-	-
H6	18	9	255	70.73	-	-
H7	12	10	213.5	58.76	-	-
M8	7	2	177.5	66.31	-	-
			Localidad de San Miguel			
H9	39	8	847.5	144.88	46.12	136.78
H10	43	8	2,450	245.68	37.75	136.69
M11	38	8	1,191	132.06	-	-
M12	63	8	1,274	182.99	50.45	142.12
H13	20	9	480	88.95	-	-
M14	31	6	1,668	191.92	-	-
H16	30	9	736	112.57	-	-
H17	32	10	499	87.22	971.09	169.37

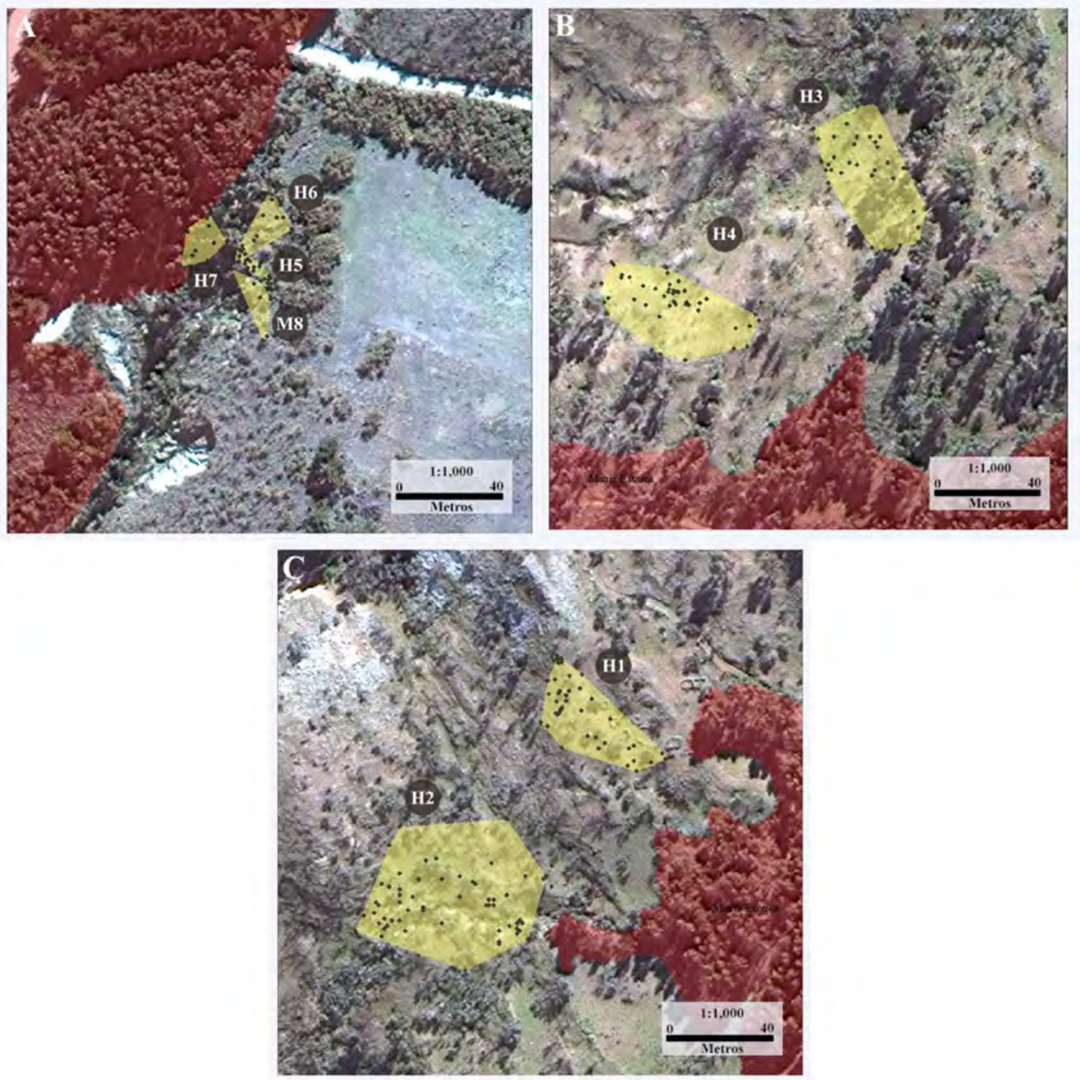

Figura 3. Ámbitos hogareños (polígonos amarillos) de la localidad de Pajcha con matriz de plantaciones de árboles exóticos (polígono rojo). A): Fragmento PAJ2, individuos H5, H6, H7 y M8. B): Fragmento PAJ1, individuos H4 y H3. C): Fragmento PAJ1, individuos H2 y H1.

puede diferir según la localidad y el tipo de bosque. La matriz de árboles exóticos igualmente tendría un efecto sobre los pequeños mamíferos como *P. osilae*. Nuestros resultados de ámbito hogareño muestran que la matriz de árboles exóticos no tendría un efecto sobre el área o perímetro, pero si sobre su movilidad; esto se evidencia en la localidad de Pajcha, con la ausencia de movimientos de *P. osilae* de los fragmentos a la matriz exótica (Figura 2). Kupfer *et al.* (2006) mencionan que una matriz opera como una barrera, filtro o conducto que variará según el tipo de perturbación, en este caso, la matriz de árboles exóticos estaría operando como una barrera. La presencia de plantaciones forestales con plantas exóticas ocasiona impactos sobre los acuíferos y perturban gravemente el ciclo de nutrientes en los suelos debido a la resistencia a la descomposición de la materia orgánica muerta (Navarro 2015). Esto se ve reflejado en la ausencia casi total de matriz de árboles exóticos en los ámbitos hogareños, a excepción del individuo H7 (Figura 2) que presenta un 33 % de matriz exótica. Por otro lado, la matriz natural de pastizal tiene un rol importante en los ámbitos hogareños de *P. osilae*. Patton *et al.* (2015) indican que esta especie está muy restringida a los hábitats de pasto dominado por el género *Stipa* en el Altiplano. La composición florística de localidad de San Miguel incluye gramíneas de este género (*Stipa ichu*), permitiendo la presencia de matriz natural de *P. osilae*, y en un caso H10 (Figura 3), el porcentaje de esta matriz es mayor que el fragmento.

Las diferencias entre los ámbitos hogareños de machos y hembras son comunes (Sanches *et al.* 2012). En ratones una característica típica es que los machos se sobrepongan con los de varias hembras (Bonatto *et al.* 2013). Bond y Wolf (1999) demostraron que en roedores microtinos (*Microtus canicaudus*) el tamaño del ámbito hogareño de los machos esta influenciado por una combinación de la densidad, acceso a las hembras y competencia con los machos. Bonnatto *et al.* (2012) determinaron en el ámbito hogareño de *Akodon azarae* los machos se evitan unos de otros, esta evasión espacial reflejaría la competencia entre los machos por monopolizar a las hembras receptivas, haciéndolos más vulnerables a ser depredados, razón por la cual se capturaron pocos individuos machos (*n* = 4). Los ámbitos hogareños de la localidad de Pajcha están conformados en su mayoría por hembras (*n* = 6; Figura 2), donde se observa que el 100 % de presencia de árboles

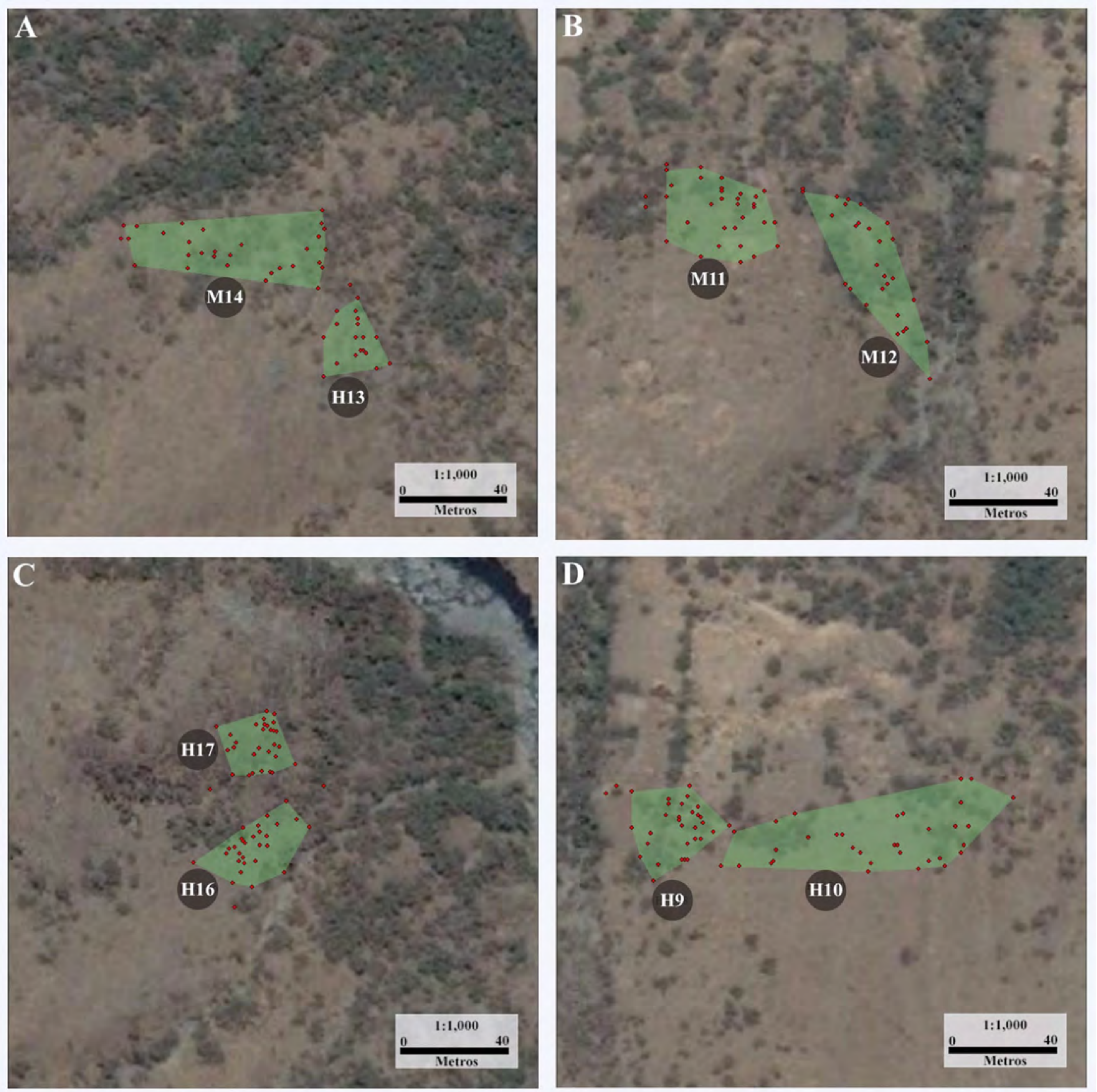

Figura 3. Ambitos hogareños (polígonos verdes) de la localidad de San Miguel con matriz de pastizales. A): Fragmento SM11, individuos M14 y H13. B): Fragmento SM11, individuos M11 y M12. C): Fragmento SM13, individuos H17 y H16. D): Fragmento SM11, individuos H9 y H10.

de *P. subtusalbida*, esto indicaría que los fragmentos de esta especie es un hábitat con abundantes recursos para pequeños mamíferos como *P. osilae*.

La generación de información sobre aspectos de la reproducción de *Polylepis* podría ayudar, en alguna medida, a remediar el problema de la fragmentación de estos bosques (Vega *et al.* 2018). La dispersión de semillas por el viento puede predominar en algunas especies de *Polylepis* (Simpson 1979), pero la superficie de los frutos de diferentes especies tiene crestas, bultos, espinas o alas, lo que también sugiere la dispersión animal (Simpson 1986). Balderrama (2013, com. pers.) encontraron que *P. osilae* consume semillas de *P. subtusalbida*, además, determinaron el grado de daño causado a las semillas y registraron que el consumo parcial sería la principal forma de *P. osilae* para consumir semillas. También registraron que en fragmentos de bosques de *P. subtusalbida* con matriz de pastizal natural y plantaciones de árboles exóticos, *P. osilae* es la especie dominante en la estructura de la comunidad de roedores. Conocer aspectos de la biología de *Polylepis*, así como sus interacciones planta-animal son de mucha importancia, ya que roedores como *P. osilae* pueden estar incrementando la probabilidad de germinación de semillas y permitiendo la distribución de semillas hacia lugares donde la vegetación

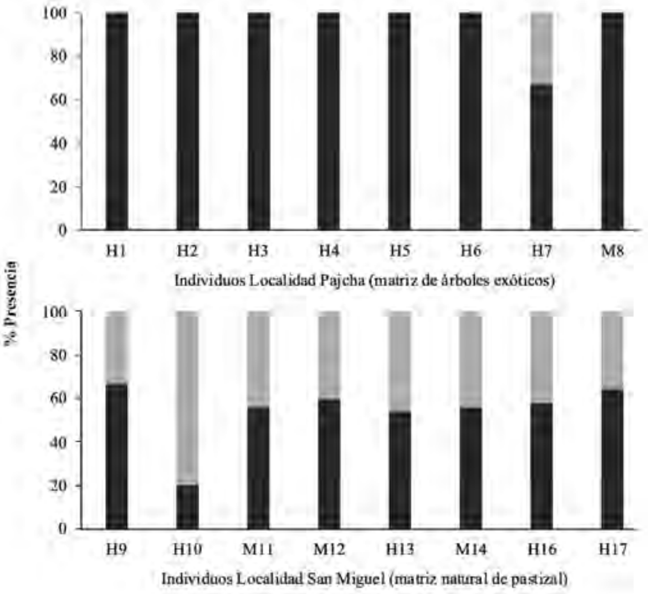

Figura 4. Porcentajes de presencia de *Polylepis subtusalbida* (color negro) y matriz (color gris) dentro los ámbitos hogareños de *Phyllotis osiale*.

natural ha sido removida, cumpliendo un rol importante en la recuperación y conservación de estos ecosistemas. Por lo anterior, conocer aspectos de su historia natural como su ámbito hogareño es de mucha importancia, al igual que sus respuestas a la fragmentación para predecir su propio destino y el de los bosques de *Polylepis*.

Agradecimientos

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Postcranial skeleton of *Spalacopus cyanus* (Rodentia: Octodontidae): description and functional aspects

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The genus *Spalacopus* includes only one species, *S. cyanus*, endemic to central Chile and one of the species best adapted to a subterranean lifetyle in the family Octodontidae. It is a member of the lineage consisting in *Octodontomys* as a sister clade containing *Octodon* and of a clade represented by *Spalacopus* and *Aconaemys*. Although the external and cranio-dental morphology have been well studied, little is known of the postcranial morphology of *S. cyanus*. Because of the peculiarities of its lifestyle and locomotion among the members of the family, it is interesting to characterize details of the morphology of the postcranial skeleton of this species and to infer their functional aspects of the morphology. Twenty-nine specimens with postcranial material stored in two collections were studied: Museo de La Plata (MLP), La Plata, Buenos Aires, Argentina and Colección de Mamíferos del Instituto de Ciencias Ambientales y Evolutivas (UACH), Universidad Austral de Chile, Valdivia, Chile. To describe in detail the morphology of the bone elements, the skeleton was divided in the following regions: axial skeleton, scapular girdle and forelimb, and pelvis girdle and hindlimb. The structures included in the axial skeleton were mainly described in cranial-caudal orientation and the limbs in proximal-distal orientation. All structures were observed with stereoscopic microscopes Leica Wild M3Z and Nikon SMZ 745T including pictures to illustrate the descriptions. Highly conservative characteristics among members of the family Octodontidae were observed in the postcranial morphology of *S. cyanus*, although some characters are exclusive to this species. The axial skeleton has seven cervical vertebrae, 12 or 13 thoracic, six or seven lumbar, four sacral, 16 to 18 caudal vertebrae, 12 or 13 ribs and a sternum with five sternebrae. The elements of the scapular and pelvic girdles as well as forelimbs and hindlimbs are described in detail, except the carpus and tarsus due to their poor state of conservation, or because they not available. The morphological pattern observed in the postcranial skeleton of *S. cyanus* conforms to a typical anatomical plan for terrestrial species, and some bones (mainly humerus and ulna) present characteristics associated with digging. The information obtained provided will allow a better interpretation of the postcranial attributes, functionally related with different lifestyle, in a future, as well as the evolution of the traits in a phylogenetic context.

El género *Spalacopus* incluye una sola especie, *S. cyanus*, endémica de la región central del Chile, siendo una de las especies mejor adaptada a la vida subterránea de la familia Octodontidae. Miembro del linaje que consiste en *Octodontomys* como hermano de *Octodon* y el clado representado por *Spalacopus* y *Aconaemys*. Si bien la morfología externa y cráneo-dentarias en *S. cyanus* han sido bien estudiadas, su morfología postcraneal es pobremente conocida. Por las peculiaridades de su estilo de vida y locomoción entre los miembros de la familia, es interesante caracterizar detalles de la morfología del esqueleto postcraneal de esta especie e inferir sus aspectos funcionales de la morfología. Se revisaron 29 ejemplares con material de postcráneo disponibles en dos colecciones sistemáticas: Museo de La Plata (MLP), La Plata, Buenos Aires, Argentina y Colección de Mamíferos del Instituto de Ciencias Ambientales y Evolutivas (UACH), Universidad Austral de Chile, Valdivia, Chile. Para la descripción detallada de la morfología de los elementos óseos se dividió al esqueleto en las siguientes regiones: esqueleto axial, cintura escapular y miembros anteriores, y cintura pélvica y miembros posteriores. Las estructuras incluidas en el esqueleto axial fueron descriptas principalmente en sentido cráneo-caudal y en los miembros en sentido próximo-distal. La observación de las estructuras se realizó con las lupas estereoscópicas Leica Wild M3Z y Nikon SMZ 745T, incluyendo fotografías para ilustrar las descripciones. En la morfología postcraneal de *S. cyanus* se observan características que se consideran altamente conservadas entre los miembros de la familia Octodontidae, pero algunos caracteres son exclusivos de la especie. El esqueleto axial está compuesto por siete vértebras cervicales, 12 ó 13 torácicas, seis o siete lumbares, cuatro sacras, entre 16 y 18 caudales, 12 ó 13 pares de costillas y un esternón compuesto por cinco esternebras. Los elementos óseos de las cinturas pectoral y pélvica como de los miembros anterior y posterior se describen en detalle, excepto los carpos y tarsos debido al mal estado de preservación o ausencia de los mismos. El patrón morfológico que presenta el postcráneo de *S. cyanus* se ajusta a un plan anatómico típico de especies terrestres y en algunos elementos óseos (húmero y ulna principalmente) se observan características típicamente asociadas con la habilidad excavadora. Los datos generados permitirán a futuro una mejor interpretación de los atributos postcraneales funcionalmente relacionados con los diferentes estilos de vida, evaluar sus estrategias locomotoras, así como también comprender la evolución de estos rasgos en un contexto filogenético.

Keywords: Chile, coruro, fuctional morphology, South America; subterranean rodent.

Introducción

Octodontidae es una familia de roedores de tamaño mediano (100 g in *Octomys* to 300 g in *Octodon*), restringidas al sur de Sudamérica, entre los -15° y -43° S de latitud (Reig 1989; Gallardo *et al.* 2007; Ojeda *et al.* 2013; Verzi *et al.* 2015). Se distribuyen en Argentina, Bolivia y Chile, en una gran diversidad de hábitats (Gallardo *et al.* 2007).

Dentro de Octodontidae se pueden reconocer dos linajes principales, el grupo de las ratas-vizcachas, que consiste en una división basal de *Octomys*, del grupo que contiene a *Tympanoctomys* y el otro linaje que consiste en *Octodontomys* como hermano de *Octodon* (*Spalacopus*, *Aconaemys*; Upham y Patterson 2015; Suárez-Villota *et al.* 2016). Las relaciones entre y dentro de algunos géneros permanecen sin resolver, como el caso de *Spalacopus*, *Aconaemys* y *Tympanoctomys* (Gallardo y Mondaca 2002; Honeycutt *et al.* 2003; Upham y Patterson 2012, 2015; Suárez-Villota *et al.* 2016).

La capacidad para cavar es prevalente en Octodontidae al igual que en la familia hermana, Ctenomyidae (Lessa *et al.* 2008). Además, entre los octodóntidos, el linaje que conduce a *Spalacopus* evolucionó a una vida completamente subterránea con la adquisición de numerosos cambios morfológicos alrededor de 2.2 Ma (Lessa *et al.* 2008); mientras que en ctenómidos tienen cambios acumulados asociados a la vida subterránea a lo largo de varios linajes, en un proceso que ha tomado al menos 8 Ma (Lessa *et al.* 2008). En este contexto, el estudio de adaptaciones para cavar en la anatomía del cráneo y parte del esqueleto apendicular fue ampliamente desarrollado en Ctenomyidae, pero no así en Octodontidae (Verzi 2002; Morgan y Verzi 2006; Verzi y Olivares 2006; (Lessa *et al.* 2008; Morgan y Verzi 2011; Morgan *et al.* 2017; Pérez *et al.* 2017).

El género *Spalacopus* incluye una sola especie, *S. cyanus*, endémica de la región central del Chile distribuida desde la costa hasta los 3,400 m en los Andes y desde la provincia de Copiapó hasta Ñuble (Pine *et al.* 1979; Nowak 1999; Muñoz-Pedreros 2000). *Spalacopus cyanus* posee un tamaño corporal entre 80 a 120 g (Torres-Mura y Contreras 1998) y representa una de las especies altamente adaptada a la vida subterránea de la familia Octodontidae de la cual forma parte. A diferencia de la mayoría de los mamíferos subterráneos, *S. cyanus* es social y vive en grandes colonias con un promedio de 16 individuos hasta un máximo de 26, y comparten el uso del mismo sistema de madrigueras (Begall *et al.* 1999; Lacey *et al.* 2019).

Al igual que otros mamíferos subterráneos su cuerpo es corto y robusto, y orejas de pequeño tamaño (Torres-Mura y Contreras 1998; Verzi *et al.* 2015) pero a diferencia tienen especializaciones visuales diurnas resultando en una visión eficiente comparable a la de otros roedores que viven en superficie (Vega-Zuniga *et al.* 2017). En su morfología cráneo-dentaria posee ciertas características asociadas a la función de excavación como la intensificación de la expansión lateral del ángulo mandibular y la cresta masetérica (Vassallo y Mora 2007) y la presencia de incisivos procumbentes con los alvéolos posteriormente desplazados (Lessa *et al.* 2008). Por otro lado, se han realizado investigaciones sobre el tipo de suelo como un factor determinante de su morfología, en este caso se han evaluado atributos como la resistencia a la flexión y la resistencia al corte de los incisivos, pero la dureza del suelo no resultó ser un factor determinante ya que no hay diferencias significativas entre poblaciones más costeras (suelo arenoso) respecto de poblaciones de zona de montaña (suelo rocoso; Bacigalupe *et al.* 2002).

Si bien la morfología externa y las características cráneo-dentarias de la especie se han definido y descripto en trabajos previos (Vassallo y Verzi 2001; Bacigalupe *et al.* 2002; Olivares *et al.* 2004; Vassallo y Mora 2007; Lessa *et al.* 2008), la morfología postcraneal es prácticamente desconocida, sólo se han realizado estudios de la escápula, húmero y carpos (Lessa *et al.* 2008; Morgan 2009; Morgan y Verzi 2011). Cabe destacar que el material esquelético postcraneal de *S. cyanus* depositado en colecciones es escaso comparado con el material de cráneo disponible. Resulta significativo conocer en detalle la morfología del esqueleto postcraneal de esta especie poco estudiada, debido a su particular modo de vida, única dentro de los octodóntidos. El objetivo de este trabajo es describir el esqueleto postcraneal de *S. cyanus* e inferir aspectos funcionales de su morfología tomando otros modelos desarrollados para grupos mejores estudiados como marsupiales y algunos roedores.

Materiales y métodos

Material examinado. Para la realización de este trabajo se revisaron dos colecciones sistemáticas mastozoológicas: Museo de La Plata (MLP), La Plata, Buenos Aires, Argentina y Colección de Mamíferos del Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Valdivia, Chile (UACH).

En total se examinaron 29 especímenes de *S. cyanus* con material de postcráneo completo, excepto carpos, tarsos, manos y pies. Se detallan a continuación los datos de localidad, que incluye país, provincia, departamento o comuna y localidad específica, y número de colección de los especímenes.

Chile: Choapa, Los Vilos: Los Vilos, 3 (UACH 2507, 2508, 2510). Canela: Huentelauquén, 1 (UACH 4020). Com. Quirihue, Los Remates, 2 (UACH 4017, 4018). Elqui, La Serena: Parque Nacional Fray Jorge, 1 (UACH 1844). Ñuble, Con. Quirihue, Los Remates, 22 (1 MLP 10.XI. 95.5, 21 UACH 1846, 1847, 2511, 2512, 2513, 2514, 2515, 2516, 2517, 2518, 4001, 4002, 4003, 4004, 4005, 4006, 4007, 4012, 4368, 4376, 4385).

Nomenclatura y descripción del postcráneo. Para la descripción detallada de la morfología de los elementos óseos se dividió al esqueleto en las siguientes regiones: 1) esqueleto axial: vértebras cervicales, torácicas, lumbares, sacras y caudales, costillas y esternón. 2) Cintura escapular y miembros anteriores: clavícula, escápula, húmero, radio, ulna y carpos. 3) Cintura pélvica y miembros posteriores:

pelvis, fémur, tibia, fíbula y tarsos. Para la descripción de cada estructura esquelética se consideró la forma, superficie, tamaño y orientación, incluyendo además la variación en número de los elementos óseos que la componen. Para las descripciones se siguió la nomenclatura propuesta por: Evans (1993), Argot (2001; 2002; 2003), Sargis (2001; 2002a, b), Horovitz y Sánchez–Villagra (2003), Bezuidenhout y Evans (2005), Morgan y Verzi (2006), Selthofer *et al.* (2006), Candela y Picasso (2008), Salton y Sargis (2008; 2009), Flores (2009), Flores y Díaz (2009), Morgan (2009), Carrizo y Díaz (2011). Las estructuras del esqueleto axial fueron descriptas principalmente en sentido cráneo caudal y en los miembros en sentido próximo distal.

La observación de las estructuras se realizó con lupas estereoscópicas Leica Wild M3Z y Nikon SMZ 745T. Para una mejor visualización e ilustración de los diferentes elementos postcraneales observados se tomaron fotografías con cámara digital Nikon D3200.

Resultados

En la morfología postcraneal de *S. cyanus* se observan características que se consideran altamente conservadas entre los miembros de la familia Octodontidae, pero algunos caracteres son exclusivos de la especie. A continuación, se describen de manera detallada cada elemento del esqueleto postcraneal por regiones.

Esqueleto axial. Está compuesto por siete vértebras cervicales, 12 ó 13 torácicas, seis o siete lumbares, cuatro sacras, entre 16 y 18 caudales, 12 ó 13 pares de costillas y un esternón compuesto por cinco esternebras.

Atlas. Es un elemento de aspecto ovalado, su eje transversal es más largo que el dorsoventral (Figura 1a). El arco neural dorsal es corto con el margen craneal cóncavo en forma de "U" y el caudal es recto o cóncavo, pero en forma de "V". El tubérculo dorsal es bajo, en cuatro especímenes apenas visible (UACH 2518, 4005, 4020, 4367). Los forámenes atlantales son redondeados y grandes, los procesos transversos son lobulados, y en vista lateral, no sobrepasan el nivel de las facetas caudales.

Las facetas craneales son más largas que anchas con forma arriñonada con los márgenes dorsales muy extendidos anteriormente. Las facetas caudales tienen forma subtriangular y se orientan caudomedialmente. Los forámenes transversos son grandes y redondeados a ovalados, pero no se observan en vista craneal debido al gran desarrollo de las facetas de articulación. El tubérculo ventral es pequeño terminando en una punta roma y orientado ventralmente.

Axis. La forma general es subtriangular, con los bordes del arco convergiendo dorsalmente en forma recta (Figura 1b). El proceso espinoso es alto y robusto, y sólo en un ejemplar (UACH 1844) se observó una extensión caudal sobrepasando la tercera vértebra cervical (C3); en vista lateral, el borde dorsal es redondeado y los bordes craneal y caudal curvos; en vista dorsal, el proceso se ensancha en dirección caudal.

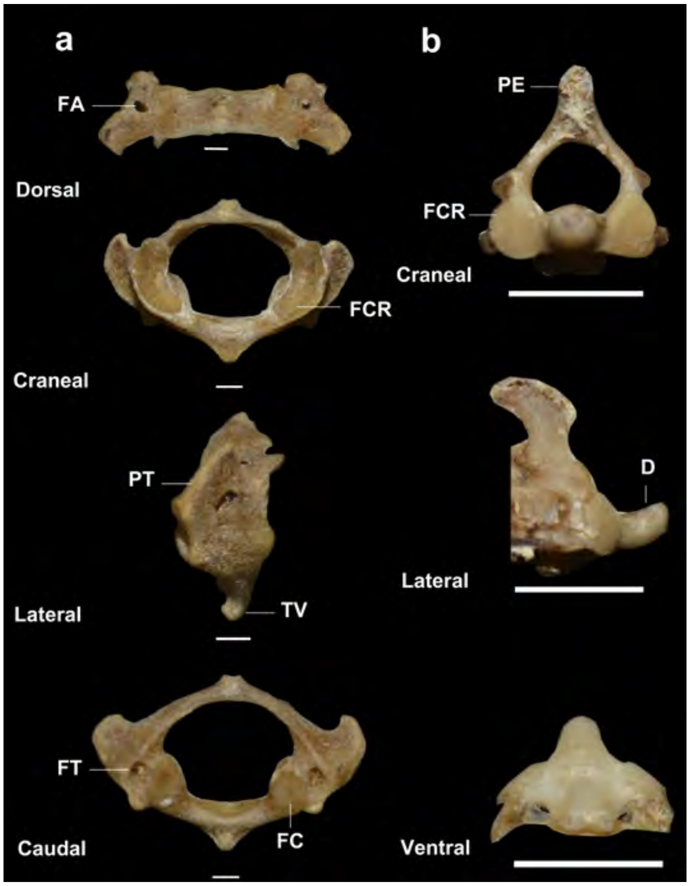

Figura 1. a) Atlas en vista dorsal, craneal, lateral y caudal. Escalas 1 mm. b) Axis en vista craneal, lateral y ventral. Escalas 5 mm. Abreviaturas: dens (D), forámenes atlantales (FA), facetas craneales (FCR), facetas caudales (FC), foramen transverso (FT), proceso espinoso (PE), procesos transversos (PT), tubérculo ventral (TV).

Las facetas de articulación craneal se orientan craneolateralmente y son subtriangulares. El proceso odontoides (dens) se orienta anterodorsalmente, es corto y conectado con las facetas craneales. Los procesos transversos terminan en punta y se extienden caudalmente llegando al nivel de las post-zigapófisis. Los forámenes transversos son grandes y redondeados.

Ventralmente, el arco vertebral es corto sin forámenes ventrales, el tubérculo ventral termina en forma bilobada. El borde caudal del axis articula imbricado con la C3.

Vértebras cervicales posteriores (C3-7). La forma general de las vértebras es baja y ancha. El tamaño de los arcos neurales de las C3 a 7 se mantienen constantes en todos los ejemplares con los bordes craneal y caudal rectos, excepto en UACH 2517 y 4002 donde el arco de la C5 es más delgado con el borde craneal cóncavo. Los espacios intervertebrales son tan anchos como el arco dorsal. Los procesos espinosos están ausentes en toda la serie cervical. Los procesos transversos son anchos y cortos desde la C3 a 5 y se dirigen caudalmente, en las C6 y 7 son más delgados y levemente más largos, la C6 mantiene la orientación caudal mientras que en la C7 son perpendiculares (Figura 2). Los forámenes transversos son grandes, redondeados y presentes hasta la C6. En la C6 se observa la lamela con forma de yunque invertido debido a la extensión anteroposterior de su borde más ventral, con la porción posterior más extendida en comparación a la extensión anterior y al arco ventral; sólo en dos ejemplares es diferente, con proyección caudal y sin extensión anterior por delante del arco ventral (UACH 2513) o con la misma extensión cráneo-caudal que el arco ventral sin proyectarse (UACH 2517).

Ventralmente, los cuerpos vertebrales muestran en las C3 y 4 un tubérculo ventral bilobado sobre el margen que contacta con la vértebra siguiente, a partir de la C5 el cuerpo es plano. No se observan forámenes en toda la serie cervical, con excepción de un ejemplar con un par pequeño en la C5 (UACH 2510). Las pre-zigapófisis se orientan dorso-medialmente con una articulación oblicua con respecto al plano sagital.

Vértebras torácicas (T1-T12 ó 13). El número de vértebras torácicas no se pudo determinar para la totalidad de los ejemplares examinados por estar la serie incompleta o por falta de limpieza de los elementos esqueléticos. En los ejemplares donde se pudo determinar el número se registraron 13 vértebras torácicas en 11 ejemplares (UACH 1846, 2514, 4002, 4003, 4005, 4006, 4012, 4017, 4018, 4376, 4385) y 12 vértebras en ocho especímenes (UACH 1844, 2510, 2513, 2518, 4001, 4020, 4367, 4368).

En vista dorsal, la forma general de las vértebras es similar a las cervicales hasta la T3, a partir de la T4 se estrechan, aumentan el largo cráneo-caudal siendo transversalmente más cortas. El proceso espinoso en la T1 es pequeño, en la T2 alcanza el máximo desarrollo, en la T3 disminuye su altura, en la T4 es más alto que la T3 aumentando gradualmente la altura hasta las T8 y 9, con algunas excepciones tales como un ejemplar (UACH 2513) donde las T3 y 4 tienen los procesos muy bajos e iguales entre sí. En relación a la orientación es vertical hasta las T3 y 4 y a partir de la T5 es caudal hasta la T9 (Figura 2). La forma, en vista lateral, tienen poca extensión cráneo-caudal hasta la T8, y en la T9 está más extendido que en las anteriores. Los procesos de las dos últimas torácicas tienen forma similar a las vértebras lumbares. Las vértebras diafragmática y anticlinal se ubican en la T10, a partir de la cual la altura del proceso espinoso se reduce notablemente e invierten su orientación en sentido craneal (Figura 2).

En la T1, los procesos transversos son latero-ventrales, desde la T2 a la T12 ó 13 los procesos transversos se van acortando y su orientación es cráneo-dorsal. Las facetas costales, donde articula el primer par de costillas, tienen forma de ventosa hasta la T9 y a partir de la T10 se reducen a una pequeña protuberancia. Dicha faceta se mantiene sobre los procesos transversos hasta la T4, a partir de la T5 se comienza a separar gradualmente hasta separarse completamente en la T8. Los procesos accesorios se observan a partir de la T9 como una proyección caudal en paralelo con el eje cráneo-caudal y en contacto con los procesos transversos; a partir de la vértebra anticlinal (T10) se separan del proceso transverso. En vista ventral, los cuerpos de las vértebras son en general planos y a partir de la T6 son levemente convexos. Uno a dos forámenes pueden estar presentes en algunas vértebras a lo largo de la serie torácica.

Vértebras lumbares (L1-6 ó 7). El número de la serie lumbar varía, al igual que con las vértebras torácicas en 11 especímenes se registran seis lumbares (UACH 1846, 2514, 4002, 4003, 4005, 4006, 4012, 4017, 4018, 4376, 4385) y en ocho (UACH 1844, 2510, 2513, 2518, 4001, 4020, 4367, 4368) se registraron siete lumbares. La primera lumbar se identifica por la ausencia de fóveas costales articulares.

Las vértebras lumbares son cuadrangulares, robustas y su tamaño aumenta hasta la L5 y luego disminuye en la L6 ó 7 (Figura 2). Los procesos son bajos y se dirigen cranealmente, pero no se extiende por delante de la articulación vertebral, sólo en la última lumbar es levemente más alto. Los procesos transversos se orientan cráneo-ventralmente con forma de aleta con la porción proximal ancha y la distal más estrecha; son cortos en las primeras lumbares y levemente más largos en las L6 y 7. Los procesos accesorios, separados de los transversos, están bien desarrollados y se observan hasta la L6. Los procesos mamilares están presentes en todas las lumbares, son muy bajos, pequeños y proyectados hasta el nivel de las facetas articulares craneales. La articulación entre la pre- y la post-zigapófisis es latero-medial.

Vértebras sacras (S1-4). Todos los ejemplares examinados presentan cuatro vértebras sacras, en la mayoría de los ejemplares están fusionadas completamente entre sí desde la S1 a 3, mientras que entre las S3 y 4 la fusión es incompleta (Figura 2); sólo en un espécimen hembra la fusión no es completa entre ninguna de las vértebras sacras (UACH 2510). Los procesos transversos están fusionados formando una lámina. Los procesos espinosos, prácticamente en la totalidad de los ejemplares, no se fusionan entre sí, sólo en dos individuos se registra la fusión entre los procesos de la S1 y 2 (UACH 2513, 4020). El proceso espinoso de la S1 es el más alto y orientado cranealmente, los otros tres son perpendiculares. Las crestas sacras intermedias son evidentes.

Dorsalmente, los forámenes sacrales son pequeños y redondeados, se observan sólo dos pares debido a que la articulación entre la S3 y 4 estaba rota en todos los ejemplares examinados; el primer par es más pequeño que el segundo. Ventralmente no se observa el promontorio y se pueden observar pequeños forámenes.

Vértebras caudales (Ca1-18 ó 19). *Spalacopus cyanus* es una especie de octodóntido de cola corta, en la mayoría de los especímenes se registraron 19 vértebras caudales (UACH 2517, 4001, 4009, 4012, 4018, 4367), en cuatro 18 (UACH 1846, 2513, 2518, 4006) y en el resto de los ejemplares la serie caudal estaba incompleta. Las dos primeras caudales son similares a la última vértebra sacra, en la Ca3 se reduce la extensión lateral de los procesos transversos y el tamaño de la vértebra (Figura 2). La articulación entre pre- y post-zigapófisis se observa entre las tres primeras vértebras caudales, es reducida entre las Ca3 y 4, y a partir de la Ca4 la articulación de la porción posterior ocurre entre el cuerpo vertebral y los discos intervertebrales. Los procesos espinosos se observan bien desarrollados en las Ca1 y 2, a partir de la Ca3 se reducen y son visibles sólo hasta las Ca8 y 9.

Los procesos transversos están expandidos lateralmente hasta la Ca4 a partir de la cual se acortan, alcanzando la misma longitud del cuerpo vertebral en la Ca5, siendo sólo pequeñas protuberancias apenas extendidas lateralmente hasta la Ca10. En vista ventral, a partir de la Ca3 se observa el proceso hemal muy pequeño cerrado en forma de canal hasta la Ca5, a partir de la Ca6 está abierto y adquiere una forma de "H". Dichos procesos van disminuyendo en tamaño hacia las últimas vértebras y se observan hasta el final de la serie caudal conservando la forma en "H".

Costillas. Once especímenes presentan 13 pares de costillas (UACH 1846, 2514, 4002, 4003, 4005, 4006, 4012, 4017, 4018, 4385, 4376) y en ocho 12 (UACH 1844, 2510, 2513, 2518, 4001, 4020, 4367, 4368). Cabe destacar que en un individuo se registró una anomalía con 13 costillas de un lado y 12 del otro (UACH 2517). El primer par de costillas es el más corto, robusto, con el borde medial cóncavo y el lateral convexo y con el extremo ventral aún más robusto y ancho. El resto de las costillas se comprimen y se vuelven progresivamente más largas, alcanzando el máximo de

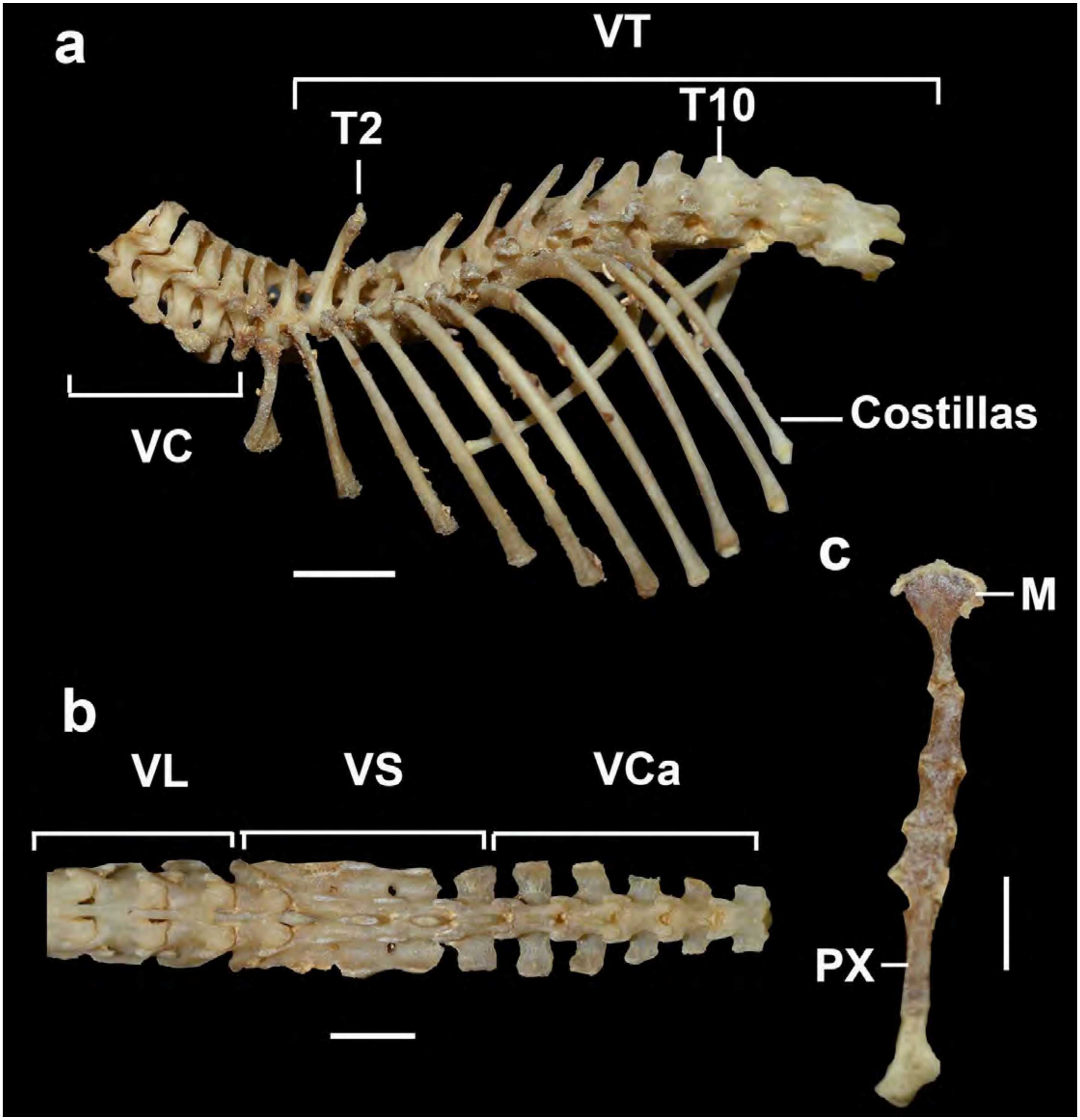

Figura 2. a) Vértebras cervicales y torácicas y costillas en vista lateral. b) vértebras lumbares, sacras y caudales en vista dorsal. c) esternón en vista ventral de *S. cyanus*. Abreviaturas: manubrio (M), proceso xifoides (PX), segunda vértebra torácica (T2), vértebra anticlinal y diafragmática (T10), vértebras cervicales (VC), vértebras caudales (VCa), vértebras lumbares (VL), vértebras sacras (VS), vértebras torácicas (VT). Escalas 5 mm.

longitud en el séptimo u octavo par, y a partir de estos pares se acortan nuevamente (Figura 2). Las primeras cinco costillas presentan un cuerpo aplanado en su porción más dorsal y cilíndrico sobre su mitad ventral, hacia el final de la serie el cuerpo completo se vuelve más cilíndrico. El cuello es corto en las cuatro o cinco primeras costillas, del sexto al noveno o décimo par se alarga y en las últimas tres costillas se simplifica toda la estructura y no hay una distinción clara del cuello, entre la cabeza y el tubérculo costal. El tubérculo costal tiene su máximo desarrollo en el primer par de costillas, se mantiene bien desarrollado hasta el cuarto o quinto par y luego se reduce, pero se observa hasta el último par de costillas.

Esternón. El esternón está compuesto por cinco esternebras incluyendo manubrio y xifoides. El manubrio es la estructura de mayor tamaño y no presenta quilla, su porción anterior es aplanada en forma de abanico con el borde anterior curvo con expansiones laterales y la porción posterior es alargada y relativamente cilíndrica, lo que le da la forma de "T"; sólo en dos ejemplares las expansiones laterales de la porción anterior del manubrio son mayor y la forma se asemeja a un martillo (UACH 2510, 4002). La segunda esternebra presenta la porción anterior más angosta que la posterior, la tercera y cuarta esternebras tienen forma rectangular, estas tres son aplanadas y cortas representando aproximadamente la mitad del largo del manubrio. El xifoides es la segunda esternebra más larga, delgada y aplanada, con el cartílago xifoides en su extremo caudal, con la porción caudal extendida.

Cintura escapular y miembros anteriores; clavícula. La clavícula es delgada y sigmoidea con la curvatura más marcada hacia el extremo escapular. El extremo esternal es robusto y cilíndrico con la faceta articular esternal redondeada y el extremo escapular achatado con la faceta escapular alargada y plana.

Escápula. La escápula tiene forma triangular con los bordes craneal (o superior) y caudal (axilar o lateral) más largos que el borde vertebral (Figura 3a). La superficie lateral está dividida por la espina escapular en una fosa supraespinosa de menor tamaño que la infraespinosa. El borde craneal es sigmoideo, la curvatura es más marcada hacia el cuello de la escápula, el borde vertebral es curvo a levemente recto y el caudal es recto con un ángulo caudal más o menos evidente. La espina escapular se separa del cuerpo escapular aproximadamente a partir de la mitad posterior de la superficie lateral de la escápula, posee una leve curvatura en su extensión hacia el borde caudal y se extiende ventralmente sobrepasando la cavidad glenoidea. La espina se continúa en un ancho y romo acromion y un delgado y puntiagudo metacromion. La superficie costal presenta una leve concavidad en la mitad de su extensión sobre la línea que divide las fosas, antero-ventralmente se enangosta donde se continua con el cuello que la separa de la cavidad glenoidea, esta última es ovalada. El proceso coracoides se extiende levemente en dirección antero-medial; en vista articular termina en un extremo redondeado, con una excepción observada en un ejemplar (UACH 4020) donde el proceso se encuentra más extendido y terminando en un extremo puntiagudo.

Húmero. La diáfisis es cilíndrica y recta. La cabeza humeral, en vista proximal, es redondeada terminando posteriormente en un pico caudal redondeado (Figura 3b). Los tubérculos mayor y menor no sobrepasan la altura de la cabeza humeral y están separados por un surco bicipital ancho y marcadamente cóncavo. Los tubérculos están bien desarrollados, el mayor más grande que el menor. El tubérculo mayor se ubica cráneo-lateralmente a la cabeza y es redondeado en vista lateral, sobre este tubérculo y proximalmente a la tuberosidad lateral humeral en una superficie central redonda y cóncava se inserta el *M. infraspinatus*. El tubérculo menor también es redondeado y se ubica medialmente a la cabeza. La cresta deltoidea se ubica por encima de la mitad de la diáfisis, está desplazada proximalmente y bien desarrollada, con una marcada extensión anterolateral y bordes redondeados.

En la epífisis distal, la cresta lateral epicondilar está extendida tanto lateralmente como próximo-distalmente con una curvatura evidente (Figura 3b vista distal). El foramen supratroclear está presente en la mayoría de los ejemplares y su desarrollo es variable, puede ser muy grande (UACH 1844, 1846, 2510, 2517, 2518, 4001) o más pequeño (UACH 4005, 4006, 4020, 4368) y en tres ejemplares (UACH 2513, 4002, 4020) está cerrado o ausente. El epicóndilo medial es mucho más grande que el lateral pero ninguno se extiende superando el borde distal de la tróclea. La tróclea presenta un mayor desarrollo próximo-distal y menor latero-medial comparado con el capítulo. La transición entre tróclea y capítulo es evidente en vista anterior, mientras que en vista posterior no se observa una división sino una única superficie en forma de polea. El capítulo tiene, en general, forma cilíndrica, aunque puede ser más redondeado; el margen lateral está engrosado, dando lugar a la cresta lateral la cual está apenas extendida por encima del borde proximal del capítulo y una cresta medial más pronunciada distalmente y orientada de manera oblicua. La fosa radial es más profunda que la del olecranon.

Radio. La diáfisis es cilíndrica, más robusta hacia el extremo distal. La articulación proximal del radio tiene forma ovalada con la superficie articular plana, el borde lateral es más redondeado que el medial con una muesca en el borde anterior. La diáfisis proximal presenta un cambio en la dirección del eje principal por debajo del nivel de la articulación proximal con la ulna; a su vez en vista anterior también se observa una marcada curvatura sobre la porción distal en dirección medial. Sobre la cara caudal medial, por debajo de la epífisis proximal, se observa la tuberosidad radial, poco desarrollada.

La epífisis distal es más robusta que la proximal, muestra una superficie articular carpal cóncava y ovalada, el eje principal está orientado craneomedial-caudolateralmente. Sobre el lado medial se observa un surco estrecho y corto próximo-distalmente para el paso del

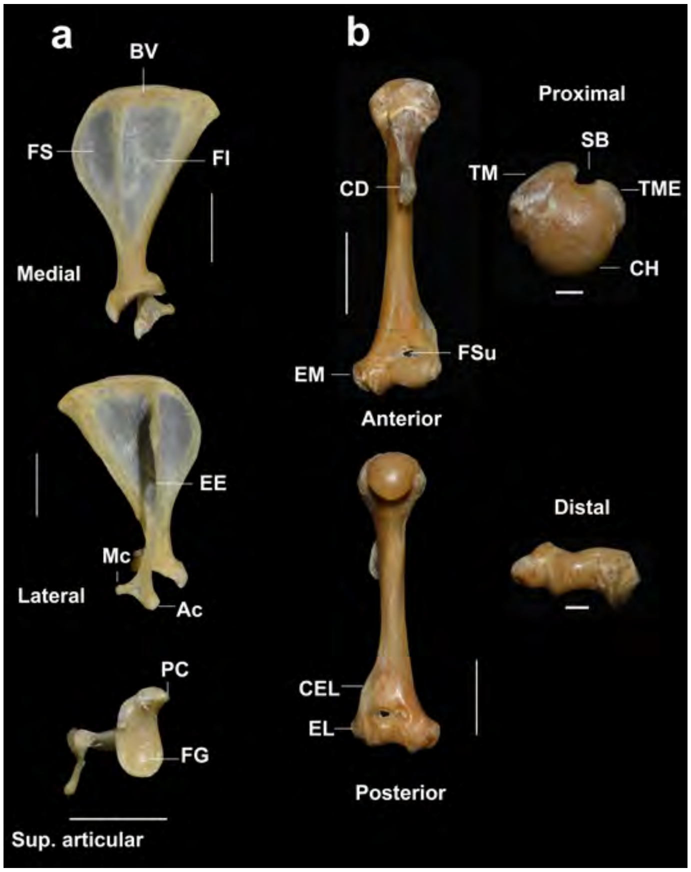

Figura 3. a) Escápula en vista medial, lateral y superficie articular. b) Húmero en vista anterior, posterior (escalas 5 mm), proximal y distal (escalas 1 mm). Abreviaturas: acromion (Ac), borde vertebral (BV), cresta deltoidea (CD), cresta epicondilar lateral (CEL), cabeza humeral (CH), espina escapular (EE), epicóndilo lateral (EL), epicóndilo medial (EM), fosa glenoidea (FG), fosa infraespinosa (FI), fosa supraespinosa (FS), foramen supratroclear (FSu), metacromion (Mc), proceso coronoides (PC), surco bicipital (SB), tubérculo mayor (TM), tubérculo menor (TME).

M. abductor digiti I longus. El proceso estiloides es pequeño, se expande latero-medialmente y apenas distalmente.

Ulna. En la epífisis proximal, el olecranon está moderadamente desarrollado cráneo-caudalmente, es relativamente largo próximo-distalmente y robusto con una zona deprimida o cóncava en la cara medial; representa, en promedio, el 17 % de la longitud total de la ulna; la tuberosidad del olecranon se engrosa medialmente hasta su margen caudal con una proyección medial muy evidente. El margen craneal del olecranon es cóncavo, el proximal convexo y el caudal prácticamente recto. La muesca o incisura troclear es profunda, con forma de "C". El proceso anconeal está definido por dos crestas: la cresta ulnar lateral proximal (ulptc) y la cresta ulnar medial proximal (umptc); en vista craneal, ambas crestas se observan continuas, sin distinguirse un punto de inflexión entre ambas. La umptc se orienta oblicuamente y no supera un ángulo de 30° con el eje próximo-distal. La ulptc tiene una gran expansión sobre la cara lateral mayor que la umptc sobre la cara medial. La muesca radial es ancha, cóncava y el eje mayor es oblicuo respecto de la diáfisis. El proceso coronoides medial está más desarrollado que el lateral, protruye anteriormente y además se proyecta medialmente en toda su extensión próximo-distal. Por debajo del proceso coronoides medial se observa una marcada fosa en vista medial proximal.

En la epífisis distal, se observan la faceta articular para el radio dispuesta medialmente y el proceso estiloides más desarrollado cráneo-caudalmente que latero-medialmente con el extremo distal redondeado y un surco sobre la cara lateral. La superficie articular se dispone disto-medialmente siendo su límite lateral el proceso estiloides propiamente dicho.

Cintura pélvica y miembros posteriores; pelvis. El ilion es más largo que el isquion, se observan alineados en vista lateral y articula con el ala de sacro (Figura 4a). El ala del ilion es larga, delgada y cóncava. El extremo anterior del ilion es recto con una leve curvatura lateral. La línea gluteal divide la superficie gluteal en una fosa gluteal (superficie gluteal dorsal) y una fosa ilíaca (superficie gluteal ventral), ambas fosas tienen un desarrollo similar, siendo la gluteal más cóncava. Cranealmente la línea gluteal se continúa lateralmente y termina en la tuberosidad coxal pobremente desarrollada dándole un aspecto redondeado al extremo craneal y caudalmente termina antes del acetábulo. Sobre el borde dorsal del ala se observa la tuberosidad sacral, levemente evidente. Caudalmente a la tuberosidad, el borde del ilion forma la incisura isquiática mayor, más larga en aquellos individuos donde se registra un ala dorsal más corta (UACH 2517, 4005, 4367, 4368).

En el cuerpo del isquion se puede observar la muesca isquiática menor, sin la presencia de una espina isquiática por delante, inclinada hacia los laterales, continuándose con los bordes caudales que se extienden marcadamente hacia los lados. La tuberosidad isquiática está bien desarrollada. La rama isquiática está curvada en forma sigmoidea.

En el cuerpo del pubis las ramas craneales se extienden dorso-lateralmente desde el cuerpo hacia la región del acetábulo y constituyen el borde craneal de la pelvis sin una eminencia iliopúbica, pero con un marcado proceso pectíneo en algunos ejemplares (UACH 2513, 2517, 4005, 4006, 4020, 4367) y ausente en tres (UACH 4002, 4368, 4385). Las ramas caudales, derecha e izquierda, se fusionan en una línea media formando la sínfisis pélvica. La sínfisis pélvica es muy corta comparada con el foramen obturador. Y en vista caudal, el arco isquiático tiene forma de "U" muy abierta por la expansión lateral de los bordes caudales. El acetábulo es redondeado e interrumpido caudalmente por la incisura acetabular, la fosa acetabular es profunda y la superficie lunate está bien delimitada. La tuberosidad femoralis está ausente. El foramen obturador es ovoide, el eje cráneo-caudal tiene menor longitud comparado con el dorsoventral y el ángulo de la rama caudal es obtuso.

Se observó dimorfismo sexual en algunas estructuras de la pelvis. Las ramas caudales del pubis en las hembras son más robustas y más altas que en los machos, mientras que las craneales son más delgadas. Una particularidad registrada es la presencia de proceso pectíneo sólo en las hembras.

Fémur. El fémur es robusto con la diáfisis levemente curvada en sentido lateral en la zona media por lo que el borde medial es ligeramente cóncavo y cilíndrica en sección transversal (Figura 4b). En la epífisis proximal, la cabeza femoral es esférica y orientada dorso-medialmente con un cuello muy corto y un surco dorsal ancho y en "U" entre el cuello y el trocánter mayor. En vista medial, la fóvea capitis se encuentra situada próxima al margen dorsal de la cabeza. Los trocánteres mayor y menor están bien desarrollados, el mayor es robusto, sobrepasa dorsalmente la altura de la cabeza y está inclinado cranealmente y en menor grado medialmente; en vista dorsal, se observa un pequeño surco en la superficie próxima al borde craneal. El trocánter menor está orientado póstero-medialmente, es de menor tamaño que el trocánter mayor y sobresale medialmente en vista caudal. En vista caudal, se observa una muy profunda fosa trocantérica que no se extiende proximalmente más allá de la altura de la cabeza y distalmente llega al nivel de la base del cuello. El tercer trocánter se localiza proximalmente sobre la diáfisis y está poco desarrollado, apenas sobresale lateralmente y en cuatro ejemplares está ausente (UACH 2517, 2518, 4001, 4006).

La epífisis distal es ancha, y la tróclea femoral se encuentra delimitada por dos crestas paralelas, medial y lateral. La superficie de la tróclea es ancha, cóncava y, en el área proximal, se extiende levemente sobre la cara craneal de la diáfisis. Los cóndilos son paralelos y separados cranealmente por la tróclea y caudalmente por una profunda y estrecha fosa intercondilar. En vista distal, el cóndilo lateral es más ancho o más extendido lateralmente que el cóndilo medial; ambos se proyectan en sentido caudal, en la mayoría de los ejemplares el medial se extiende algo más que el lateral, sólo en dos ejemplares se observan igualmente proyectados (UACH 1844, 4006). En esta vista, el desarrollo cráneo-caudal de la tróclea es mayor a la proyección caudal de los cóndilos. Las facetas para la articulación de los sesamoideos supracondiloideos están bien delimitadas.

Tibia (Figura 4c). La tibia es robusta con la porción proximal triangular en sección transversal y siendo aproximadamente un 12 % más larga que el fémur. En el primer tercio proximal, la diáfisis tiene una marcada curvatura en dirección medial. En vista proximal, los cóndilos lateral y medial son piriformes y levemente cóncavos y, en vista anterior, están al mismo nivel. El cóndilo lateral es más ancho y cóncavo que el medial, y se continúa caudo-lateralmente con la superficie articular con la fíbula. En vista proximal, el área intercondilar craneal tiene poca extensión cráneo-caudal terminando en una tuberosidad tibial bien desarrollada. El área intercondilar caudal es estrecha y cóncava. En vista caudal, se observan sobre la diáfisis dos crestas, la lateral y una medial a esta última. La lateral se origina de la zona caudal de la diáfisis y la recorre hasta la zona de articulación con la fíbula donde se inserta el *M. flexor digitorum lateralis*. La segunda cresta es más marcada en su porción proximal y hacia la mitad de la diáfisis es más baja. La muesca poplítea es una superficie estrecha y superficial. La cresta tibial está poco desarrollada sin una evidente proyección antero-medial.

La epífisis distal presenta dos facetas astragalotibiales separadas por una cresta o elevación más evidente, son ovaladas, con la medial más ancha, corta y marcadamente más cóncava que la lateral. En vista caudal, el borde caudal es curvo con el proceso tibial distal posterior poco desarrollado, comparando con el resto de los octodóntidos es el de menor tamaño. El maléolo medial, en vista medial, es redondeado y pequeño, menos proyectado distalmente en comparación con el proceso posterior. En el material examinado no fue posible observar la presencia de surcos por el mal estado en que se encontraba del material examinado.

Fíbula (Figura 4c). La fíbula es bastante más delgada que la tibia, aplanada en su porción proximal y comprimida en toda su extensión. La cabeza articular tiene forma similar a un abanico, muy aplanada, resultando en una estructura muy simple sin surcos ni tubérculos. En la unión proximal con la tibia se observa un foramen redondeado. La fusión de la fíbula con la tibia no es ósea.

El extremo distal de la fíbula no se pudo describir en detalle por las condiciones en la que se encontraba el material examinado. El maléolo fibular lateral tiene forma bilobada, es redondeado en el punto distal de contacto con la tibia, proyectado distalmente al mismo nivel del maléolo medial.

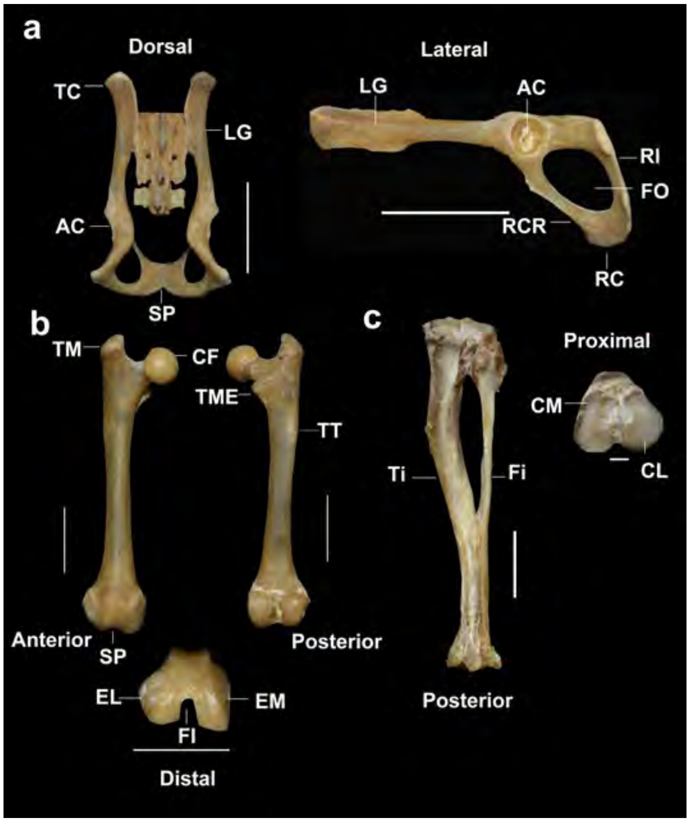

Figura 4. a) Pelvis en vistas dorsal y lateral. Escalas 10 mm. b) Fémur en vistas anterior, posterior y distal. Escalas 5mm. c) Tibia y fíbula en vistas posterior y vista proximal de la tibia. Escalas 5 mm. Abreviaturas: acetábulo (AC), cabeza femoral (CF), cóndilo medial (CM), cóndilo lateral (CL), epicóndilo lateral (EL), epicóndilo medial (EM), fíbula (Fi), fosa intercondilar (FI), foramen obturador (FO), línea gluteal (LG), rama caudal (RC), rama craneal (RCR), rama isquiática (RI), sínfisis pélvica (SP), tuberosidad coxal (TC), tibia (Ti), trocánter mayor (TM), trocánter menor (TME), tercer trocánter (TT), surco patelar (SP).

Discusión

En este trabajo, se describen por primera vez la mayoría de los elementos esqueléticos del postcráneo de *Spalacopus cyanus*, a través de dicha descripción se pudo inferir que su patrón morfológico se ajusta a un plan anatómico típico de especies terrestres. Estos resultados son consistentes con lo observado en otros mamíferos (roedores y marsupiales), como por ejemplo la ausencia de quilla en el manubrio del esternón, la extensión posterior del húmero formando un pico, los tubérculos del húmeros sin sobrepasar la cabeza humeral, la forma redondeada del acetábulo de la pelvis, la extensión del tercer trocánter por encima de la cabeza del fémur (Hatt 1932; Sargis 2002a, b; Argot 2003; Candela y Picasso 2008; Flores y Díaz 2009; Olivares 2009; Carrizo y Díaz 2011). Asimismo, en algunos elementos óseos se observan características que se corresponderían con una habilidad excavadora, principalmente en los huesos largos.

Es importante señalar que, a pesar de ser el orden más diverso de mamíferos, existen grandes faltantes de información sobre la anatomía esquelética postcraneal de los roedores. Pocos autores han realizado estudios descriptivos clásicos del postcráneo de mamíferos, pero de este tipo de investigaciones han surgido aportes muy valiosos sobre anatomía funcional, filogenia y evolución, aunque mayoritariamente en el área de paleontología (*e. g.*, Argot 2001, 2002, 2003; Szalay y Sargis 2001; Candela y Picasso 2008; Ercoli 2015); y en menor medida sobre la mastofauna actual (*e. g.*, Evans 1993; Bezuidenhout y Evans 2005; Flores 2009; Flores y Díaz 2009; Carrizo 2011; Carrizo y Díaz 2011; Salton y Sargis 2008, 2009; Candela *et al.* 2017; Gaudioso *et al.* 2017; Pérez *et al.* 2017; Pérez 2019). Muchos investigadores coinciden en afirmar que incrementar este tipo de trabajos permitirá una mejor interpretación de los atributos postcraneales funcionalmente relacionados con los diferentes estilos de vida, evaluar sus estrategias locomotoras, como así también la evolución de estos rasgos en un contexto filogenético.

A continuación, se discuten las variaciones morfológicas observadas en los elementos y en las estructuras óseas en un contexto comparativo y funcional.

Esqueleto axial. Siete vértebras cervicales y 19 toracolumbares se registran en los roedores, aunque de modo general las toracolumbares pueden presentarse como 12 y 7 ó 13 y 6 (Hatt 1932). En *S. cyanus* se presentan ambas combinaciones, siendo la de 12 y 7 la más frecuente.

En el atlas, el tubérculo dorsal en general está poco desarrollado e incluso ausente en algunos taxones. En esta región se insertan músculos que intervienen en movimientos rotacionales de la cabeza, tales como los *Mm. obliquus capitis caudalis*, *splenius* y *rectus capitis dorsalis minor* (Argot 2003; Flores y Díaz 2009); por lo tanto, en *S. cyanus* implicaría una capacidad limitada para los movimientos rotacionales. El tubérculo ventral poco desarrollado en esta especie limitaría la capacidad de movimiento del cuello en el plano sagital, relacionado con los músculos *longus colli* y *longus capitis* que se insertan en esta estructura (Argot 2003; Flores y Díaz 2009). Si bien la forma de sus facetas craneales con un buen desarrollo de los márgenes dorsales permitiría un rango más amplio de movimiento en la articulación atlanto-occipital, como se ha observado en algunos escandentios, marsupiales didélfidos, roedores sigmodontinos e incluso el resto de los octodóntidos (Sargis 2001; Argot 2003; Flores y Díaz 2009; Carrizo 2011; Pérez 2019).

En el axis, en vista dorsal dicho proceso tiende a ensancharse caudalmente terminando como en una "V" invertida o triangular, lo que proporciona una amplia superficie para la inserción del ligamento nucal, este ligamento soporta y restringe la flexión del cráneo (Sargis 2001; Argot 2003; Flores y Díaz 2009). A su vez en el proceso espinoso del axis también se insertan los músculos relacionados con los movimientos laterales y rotacionales de la cabeza (Sargis 2001; Argot 2003; Flores y Díaz 2009); y la proyección caudal de dicho proceso, si bien no es común que sobrepase la tercera cervical en esta especie, podría incrementar la ventaja mecánica de los ligamentos y músculos de esta región y actuar restringiendo los movimientos en esta región (Sargis 2001).

Los procesos espinosos en el resto de las vértebras cervicales están ausentes o levemente desarrollados, lo que restringe el área de inserción para los *Mm. spinalis cervicis y multifidus cervicis* que proporcionan los movimientos en esta región y fueron particularmente relacionados con la dieta (Argot 2003; Flores y Díaz 2009), infiriendo que aquellos mamíferos con escasa movilidad del cuello (*e. g.*, marsupiales, primates, roedores sigmodontinos) tienden a usar sus manos para llevar el alimento a la boca (Hatt 1932; Argot 2003; Carrizo 2011). Esta condición podría indicar que *S. cyanus*, como el resto de los octodóntidos, usan sus manos para capturar y llevar la comida a la boca, capacidad mencionada al menos para *T. barrerae* y cuyas vértebras cervicales, al igual que el resto de las especies de *Tympanoctomys*, carecen de procesos espinosos (Ojeda *et al.* 1996; Mares *et al.* 1997; Giannoni *et al.* 2000).

Los caracteres observados en esta región, hacen que esta especie tenga un movimiento del cuello restringido sumado a la incapacidad de ejercer fuerza con esta región dado a la presencia de características tales como: la orientación caudal de los procesos transversos hasta C5 y el escaso o prácticamente nulo desarrollo de la lamela inferior que se origina desde la C3 ó 4 hasta alcanzar su máximo desarrollo en C6. Las características señaladas contrastan con aquellas requeridas por animales con marcados hábitos predadores y con fuertes mordeduras (Argot 2003; Flores y Díaz 2009).

En la región torácica el proceso espinoso más alto se observa en T2, lugar donde se inserta el ligamento nucal y el *M. splenius* (Flores y Díaz 2009; Carrizo 2011), un buen desarrollo de este proceso permite el soporte y restringe los movimientos de la cabeza (ver Flores y Díaz 2009). En *S. cyanus*, como en los demás octodóntidos y al igual que en roedores filotinos, la vértebra anticlinal (T10-11) se observa en una posición anterior en la columna vertebral, lo que incrementa la fuerza de la musculatura epaxial, como consecuencia del cambio de inserción muscular sobre el ápice del proceso espinoso (Flores y Díaz 2009; Carrizo 2011; Pérez 2019); mientras que una posición anterior de la vértebra diafragmática (T10-11) indica un punto de unión anterior del *M. multifidus*. La posición de las vértebras anticlinal y diafragmática puede tener implicancias funcionales, ya que en estas vértebras se producen cambios relacionados con el movimiento lateral y sagital de la columna vertebral (Argot 2003; Flores y Díaz 2009). Esta ubicación en la región torácica o anterior en la columna de las vértebras anticlinal y diafragmática, puede resultar útil para los movimientos que requiere *S. cyanus* dentro del sistema de madrigueras (Reig 1989), posibilitando ciertos movimientos en el plano sagital pero con más rigidez en la flexión lateral. De igual manera no hay estudios sobre el movimiento del tronco o de la marcha de *Spalacopus cyanus*.

Los procesos espinosos y transversos de la región lumbar proporcionan los sitios de inserción para los músculos comprometidos con la flexión ventral de la columna y con la locomoción (*Mm. quadratus lumborum* y *psoas mayor*; Argot 2003; Flores y Díaz 2009). Cuando los procesos espinosos son bajos y largos (en referencia a la extensión dorso-ventral y cráneo-caudal de acuerdo Sargis 2001), lo que implica reducción de los espacios intervertebrales, la movilidad estaría restringida; mientras que los procesos largos y estrechos sumado a un mayor espacio intervertebral (Sargis 2001) permitirían mayor movilidad espinal. Los procesos espinosos en la región lumbar de *S. cyanus*, al igual que en el resto de los octodóntidos (Pérez 2019), muestran un patrón intermedio a lo planteado por Sargis (2001), con una extensión dorso-ventral mayor a lo establecido como procesos espinosos bajos, pero menor a lo que se considera como procesos altos, con espacios intervertebrales reducidos. Dicho patrón es similar a lo observado en otras formas cuadrúpedas con mayor flexión lateral y menor flexión y extensión sagital, típico de formas adaptadas al salto y contrario a lo que se produce en la región torácica de *S. cyanus* (ver Sargis 2001; Argot 2003). De igual manera, esta condición intermedia conferiría a los músculos extensores cierta ventaja mecánica para una extensión más poderosa durante la carrera terrestre con cierta capacidad de flexión y extensión vertebral para aumentar la longitud de zancada (Sargis 2001), sin mostrar variación desde los octodóntidos epigeos a subterráneos (Pérez 2019). A su vez, los procesos accesorios en *S. cyanus* se separan completamente del proceso transverso a partir de T10 y se mantienen hasta L6, se proyectan posteriormente trabando la articulación con la vértebra siguiente, lo cual restringe la flexibilidad lateral de la columna vertebral (Argot 2003). La combinación de los caracteres expuestos, hace que *S. cyanus* tenga una columna más o menos flexible, posibilitando movimientos lateral y sagital según las diferentes etapas de la locomoción.

Spalacopus cyanus es de las pocas especies de Octodontidae con cola corta, la reducción en el número total de vértebras caudales podría relacionarse con pasar más tiempo en túneles, e incluso podría asociarse con aspectos fisiológicos para evitar la pérdida excesiva de calor (ver Ercoli 2015). La articulación entre la cuarta y quinta vértebra caudal se produce a través de los discos intervertebrales, lo que aumenta la flexibilidad de la porción proximal de la cola permitiendo movimientos laterales y según lo planteado por otros autores esta condición sugiere cierta capacidad prensil (Argot 2003; Flores y Díaz 2009; Pérez 2019), aunque esta capacidad no es propia de los octodóntidos y menos aún de un animal cavador (Pérez 2019). En cuanto a la flexibilidad de la cola para movimientos laterales, podría relacionarse con el movimiento a un lado y otro como de barrido, comportamiento observado en otros roedores que se mueven hacia atrás a través del sistema de madrigueras al igual que lo plantea Reig (1970) para *S. cyanus* y las especies de *Ctenomys* (ver Stein 2000). El desarrollo de los procesos transversos y espinosos en las primeras vértebras caudales indica el buen desarrollo de los *Mm. multifidus caudal*, *ischio-caudalis* y *abductor caudal dorsalis* permitiendo movimiento en planos lateral y vertical, asociado con la capacidad de estabilizar al animal dentro de la madriguera (Stein 2000; Argot 2003; Flores y Díaz 2009; Carrizo 2011), y con la marcha atrás.

Costillas y esternón. La condición más común en el número de costillas es de 12 y algunos ejemplares de *S. cyanus* con 13 costillas; siendo estrechas en su forma no se expanden cráneo-caudalmente, morfología que se observa en formas terrestres, lo que le quitaría rigidez a la caja torácica (Sargis 2001; Argot 2003).

El esternón en *Spalacopus* está compuesto por cinco esternebras a diferencia del resto de los octodóntidos con seis esternebras, patrón que coincide con lo descrito para otros roedores y marsupiales (Bezuidenhout y Evans 2005; Flores y Díaz 2009; Carrizo 2011; Pérez 2019). Por otro lado, la quilla del manubrio está ausente y la presencia de esternebras comprimidas, indicaría un menor desarrollo del *M. pectoralis* y en consecuencia una potencia proporcionalmente reducida de los movimientos del tronco; patrón que coincide con lo descripto para roedores filotinos, sciúridos y marsupiales sin habilidades trepadoras (Bezuidenhout y Evans 2005; Flores y Díaz 2009; Carrizo 2011).

Cintura escapular y miembro anterior; clavícula. La clavícula juega un rol importante en la cintura escapular de los mamíferos, entre otras cosas por interconectar el esqueleto axial con el apendicular del miembro anterior (Rocha-Barbosa *et al.* 2002). En esta especie, tiene la forma típica de otros mamíferos (Bezuidenhout y Evans 2005; Flores y Díaz 2009) y con un desarrollo mayor comparado con roedores caviodeos donde la articulación con la escápula y el esternón se realiza por medio de ligamentos (Rocha-Barbosa *et al.* 2002). Su presencia mantiene una distancia fija entre el acromion y el manubrio, asegurando un movimiento muy preciso entre ambas estructuras

(Rocha-Barbosa *et al.* 2002) estabilizando y dando soporte al miembro anterior.

Además, en *S. cyanus*, la clavícula es sólo más sigmoidea respecto de los roedores filotinos, con los extremos esternal y escapular con igual desarrollo a diferencia, por ejemplo, de los marsupiales arborícolas donde el extremo esternal está más desarrollado (Flores y Díaz 2009).

Escápula. La escápula de *S. cyanus* y del resto de Octodontidae tiene forma subtriangular, típica de otros roedores y algunos marsupiales (Bezuidenhout y Evans 2005; Flores y Díaz 2009; Morgan 2009; Carrizo 2011; Pérez 2019). La condición, relacionada con un patrón morfológico de formas terrestres o generalizadas y, de acuerdo a otros autores, a formas arborícolas (ver Salton y Sargis 2008), es un mayor desarrollo de la fosa supraespinosa (Argot 2001; Sargis 2002a; Flores y Díaz 2009) lo que proporciona mayor superficie para el *M. supraspinatus*; esto no coincide con el patrón observado en *S. cyanus* como en el resto de las especies de la familia, donde la fosa supraespinosa tiene menor desarrollo. Por otro lado, el *M. infraspinatus* se origina en la fosa infraespinosa y es responsable de dos funciones: abducción y rotación externa del húmero, asociado a la muesca escapular permitiendo mayor estabilidad del hombro y está menos desarrollado en las formas terrestres en comparación con arborícolas (Argot 2001); y de acuerdo a la morfología observada en *S. cyanus* podría ser ventajoso para excavar, si bien no es una especialización fosorial propiamente dicha (ver Morgan 2009: 503).

En todos los miembros de la familia Octodontidae se observa que el hábito locomotor no parece ser el mayor determinante de la forma escapular a nivel de especies, en coincidencia con lo planteado por Morgan 2009. Algunas diferencias o particularidades encontradas pueden asociarse con ciertas capacidades mecánicas y funcionales que se discuten a continuación. La extensión del acromion más allá del proceso coracoides, como se observa en todos octodóntidos, permite que el *M. deltoideus* envuelva el hombro por lo que el brazo de palanca es corto debido a la proximidad del centro de rotación de la articulación (Argot 2001). La longitud del acromion en un animal excavador podría indicar si el animal está generando fuerza desde la musculatura del hombro o del antebrazo (Salton y Sargis 2008), aunque mientras que en algunos cavadores el acromion está muy desarrollado, en otros el acromion está reducido (Salton y Sargis 2008). En *S. cyanus*, el acromion está más desarrollado que el metacromion y también más desarrollado si se compara con el acromion de otras especies de octodóntidos; pero no es tan largo como en otros cavadores más especializados (Salton y Sargis 2008), lo que indicaría que posee cierta capacidad de generar parte de la fuerza con la musculatura del hombro (Salton y Sargis 2008).

El metacromion es el sitio de inserción para los *Mm. trapezius*, *atlantoscapularis* y *omotransversarius* anterior y para la extensión del *M. deltoideus pars acromialis* (ver Salton y Sargis 2008), los cuales son músculos involucrados con la estabilización escapular y la rotación humeral; sugiriendo que el metacromion, cuando está presente como en *S. cyanus*, indica el soporte de cargas pesadas en el hombro (Salton y Sargis 2008). Por lo tanto, esta especie tiene capacidad de generar fuerzas con el miembro anterior, así como también una buena estabilidad corporal.

Húmero. Algunos autores indican que la forma de la cabeza humeral no es un buen indicador de arboricoría o cursorialidad (Szalay y Sargis 2001; Candela y Picasso 2008), ya que la gran variación de este rasgo hace imposible correlacionar la forma de la cabeza con los movimientos parasagitales y rotacionales del miembro anterior con el tipo de locomoción (Candela y Picasso 2008). La cabeza humeral semiesférica de *S. cyanus* se asocia con una baja capacidad de rotación vinculado con las formas terrestres (Sargis 2002a; Argot 2003; Flores y Díaz 2009); además, se desplaza posteriormente formando un "pico" y este carácter también se encuentra asociado a formas de locomoción terrestre (Szalay y Sargis 2001). El "pico" es la estructura donde la escápula y el húmero "traban" y la articulación se vuelve más estable, a diferencia de formas arborícolas con mayor flexibilidad hacia el plano medial en esta articulación y sin un "pico" desarrollado posteriormente (Szalay y Sargis 2001).

Los tubérculos mayor y menor en *S. cyanus* no sobrepasan el nivel de la cabeza humeral, lo que permite un rango más amplio de movilidad escapular (Szalay y Sargis 2001; Candela y Picasso 2008), característica ampliamente observada en marsupiales y algunos eretizóntidos arborícolas; sin embargo, también se observa en formas terrestres de cavioideos y chinchilloideos, equímidos y octodóntidos. Debido a esta gran variabilidad, coincidimos con Candela y Picasso (2008) acerca de la imposibilidad, hasta el momento, de correlacionar la forma de la cabeza humeral con la gama de movimientos parasagitales o rotacionales de la extremidad anterior para Hystricognathi A diferencia de algunos roedores escansoriales, fosoriales y subterráneos (Stein 2000) que cuentan con una cresta deltoidea de posición más distal, *S. cyanus* presenta la cresta en la mitad proximal de la diáfisis lo que representaría una desventaja mecánica para los músculos deltoideo y pectoral que contribuyen a la retracción del miembro anterior (Stein 2000; Argot 2001; Morgan y Verzi 2006).

En la epífisis distal del húmero, la morfología del epicóndilo medial y de la cresta epicondilar lateral reflejan el tipo de locomoción (Argot 2001; Candela y Picasso 2008; Flores y Díaz 2009). En *Spalacopus*, la mayor extensión del epicóndilo medial está precisamente relacionada con la capacidad de excavar (Stein 2000; Salton y Sargis 2008), ya que la mayor extensión provee más superficie para los músculos carpales y digitales (*Mm. flexor digitorum profundus*, *flexor carpi radialis* y *flexor carpi ulnaris*) que a su vez dan mayor fuerza de flexión a la muñeca y los dígitos durante la excavación (Argot 2001; Sargis 2002a). Cabe destacar que *S. cyanus* si bien usa las patas delanteras para remover el suelo mientras excava también utiliza los incisivos (Reig 1970). La tróclea y el capítulo marcan la superficie articular con la ulna y el radio respectivamente. La forma del capítulo se correlaciona con el movimiento del radio en el húmero, una forma esférica es indicativo de movimiento multiaxial, mientras que un capítulo trocleado se correlaciona en diversos grados con la rápida flexión o extensión de la ulna que requiere refuerzo lateral (Salton y Sargis 2008). En *Spalacopus*, el capítulo muestra una evidente convexidad, lo que otorgaría mayor movilidad a la unión del codo permitiendo libre rotación del radio durante la pronación y supinación del brazo, esto podría relacionarse con la capacidad de excavar (Sargis 2002a; Candela y Picasso 2008); este atributo es similar en otros dos géneros fosoriales de Octodontidae, *Aconaemys* y *Octodon* (Pérez 2019).

Radio y ulna. El radio y la ulna están relacionados con el poder de desplazamiento de la tierra y del agua ya sea al cavar o nadar (Salton y Sargis 2008). La evidente curvatura de la diáfisis del radio, que se observa en *Spalacopus*, como en los demás octodóntidos y algunos roedores filotinos y marsupiales, indica un mayor desarrollo de los músculos comprometidos en movimientos de pronación y supinación (Argot 2001; Carrizo 2011; Pérez 2019). Esto podría sugerir que *Spalacopus*, como sus congéneres, presentan buena movilidad en las manos permitiendo manipular el alimento como ya fue mencionado anteriormente y remover el sustrato.

Respecto a la forma de la cabeza del radio, existen diferentes explicaciones. En el caso de *Spalacopus* con una cabeza elíptica u ovalada algunos autores consideran que provee más estabilidad a la articulación húmero-radial restringiendo la rotación radial y favoreciendo el movimiento en el plano sagital, característico de mamíferos terrestres (Sargis 2002a; Candela y Picasso 2008) pero otros autores consideran que una cabeza más elíptica que redondeada caracteriza a formas excavadoras (Stein 2000).

En el olecranon se inserta el *M. triceps brachii* y se correlaciona con el comportamiento locomotor en mamíferos arborícolas, terrestres y fosoriales (Van Valkenburgh 1987; Stein 2000; Argot 2001). Cuanto más largo sea el olecranon mayor es la fuerza de palanca permitiendo una fuerte extensión del miembro anterior, característico de formas excavadoras (Salton y Sargis 2008); en *Spalacopus* la ulna es más robusta y el olecranon es levemente más largo que el resto de los octodóntidos (Pérez 2019).

El tamaño relativo del proceso coronoides medial y la forma y disposición de la muesca radial se correlacionan con la preferencia locomotora (Candela y Picasso 2008). Como se describe para roedores histricomorfos terrestres, como octodóntidos, el proceso coronoides medial se encuentra reducido respecto de la muesca radial (Candela y Picasso 2008). La muesca radial con una superficie ligeramente cóncava y de disposición oblicua, como se observa en *Spalacopus*, es característica de hábitos terrestres (Argot 2001; Candela y Picasso 2008).

Cintura pélvica y miembros posteriores; pelvis. El ilion, isquion y pubis inciden en las cambiantes cargas de los miembros posteriores durante la locomoción (Salton y Sargis 2009). La forma general y el tamaño relativo, así como las rugosidades y los tubérculos en la superficie de los tres componentes, son indicadores útiles para la interpretación funcional (Salton y Sargis 2009). En líneas generales, la pelvis de *S. cyanus* no exhibe importantes especializaciones, la morfología es bastante conservada no sólo en esta especie sino en todos los octodóntidos. La morfología del acétabulo es redondeado y abierto como en las formas terrestres, lo cual restringe la movilidad de la unión de la cadera y el movimiento en el plano parasagital, lo que incrementa la eficiencia de la locomoción terrestre (Sargis 2002b). No se observaron en los ejemplares de *S. cyanus* analizados, otras características asociadas a la locomoción terrestre tales como la curvatura lateral anterior del ilion, como se observa en la mayoría de los octodóntidos y que sugiere un incremento en el área de origen del músculo *glutei* y de la musculatura epaxial al igual que en otras formas terrestres (Argot 2002) o la presencia de la tuberosidad femoralis por delante del acetábulo que incrementaría el brazo de palanca del *M. rectus femoris*, similar a lo descrito en roedores equímidos terrestres (ver Olivares 2009).

Una característica única de *Spalacopus* es la forma del arco isquiático en "U" con los bordes caudales muy expandidos lateralmente, a lo que hasta el momento no se le atribuye alguna condición funcional. En esta estructura se origina el complejo isquipúbico (*biceps femoris, semitendinosus, semimembranosus, gracilis, adductor magnus,* y *quadratus femoris*) desde el isquion posterior y el pubis, actuando como propulsores durante la primera etapa de carrera, cuando hay una resistencia considerable y se necesita mayor fuerza de empuje (Salton y Sargis 2009). A la vez que el complejo glúteo, que se origina en el ilion, es el principal responsable del golpe final en la propulsión de las extremidades posteriores, donde hay menos resistencia y mayor potencial de velocidad. La relación entre ambos complejos está dada por si el ilion es más largo que el isquion (como algunos mamíferos cursoriales y octodóntidos) o viceversa (algunos mamíferos acuáticos) y de acuerdo a esto, el complejo muscular que más enfatiza su acción (Salton y Sargis 2009). Otra característica descrita para mamíferos saltadores es la proyección dorsal del isquion, sin embargo, no es claro cuál sería la relación de la expansión lateral del isquion, como se observa en *S. cyanus*.

Fémur. *Spalacopus*, al igual que otros octodóntidos, muestra en la morfología del fémur atributos que se relacionan con las formas terrestres, tales como la cabeza femoral semiesférica y la extensión del trocánter mayor por encima de la cabeza femoral; lo que incrementaría el brazo de palanca y la ventaja mecánica de los *Mm. glutei minimus* y *medius*, favoreciendo así una fuerte y rápida extensión del muslo, condición descripta para otros roedores histricomorfos terrestres (Argot 2002; Candela y Picasso 2008;

Flores y Díaz 2009, Pérez 2019). La posición del trocánter menor posteromedial, como se observó en otros roedores histricognatos terrestres, indicaría una orientación más anteroposterior de las fibras del complejo iliopsoas (Argot 2002; Candela y Picasso 2008), el cuál actuaría principalmente como un transportador del fémur, facilitando los movimientos parasagitales (Argot 2002; Candela y Picasso 2008). Además, la orientación ligeramente más caudal del trocánter menor en formas terrestres, sugiere una abducción menos poderosa y una mayor velocidad en las formas terrestres (Szalay y Sargis 2001).

Una particularidad observada en *S. cyanus* es la poca extensión lateral del tercer trocánter, lo que podría indicar que la extremidad posterior posee cierta habilidad de permanecer flexionada, carácter que fue mencionado para algunos escandentios arborícolas con una locomoción más lenta (Sargis 2002b). Esta característica es sólo compartida con dos especies más de su familia, *A. fuscus* y *O. degus* (Pérez 2019). Además, la posición más proximal del tercer trocánter sobre la diáfisis podría indicar una función extensora más marcada del *M. gluteus superficialis* similar al *gluteus medius* (Candela y Picasso 2008), a diferencia de lo observado en eretizóntidos y otros histricognatos terrestres donde la posición del tercer trocánter es más distal. De igual manera, la posición del tercer trocánter no está claramente relacionada con la preferencia de sustrato y la posición distal sería una condición primitiva para Hystricognathi (Candela y Picasso 2008).

En *Spalacopus*, la epífisis femoral distal está más comprimida anteroposteriormente comparada con los demás octodóntidos, por lo tanto, tiene una mayor extensión transversal. Esta condición indica una flexión habitual de los miembros posteriores asociado a formas arborícolas (Argot 2002; Sargis 2002b; Candela y Picasso 2008; Pérez 2019). La extensión anteroposterior de la epífisis distal determina la morfología del surco troclear (Argot 2002). Las epífisis extendidas presentan un surco troclear estrecho, largo y bien delimitado por crestas (mayoría de los octodóntidos); mientras que en las formas comprimidas el surco es ancho, poco profundo y con crestas menos marcadas (*Spalacopus*). Una forma similar al surco de *Spalacopus* se observó en géneros de tenrecoideos subterráneos y probablemente sea indicativo de abducción lateral y rotación de la tibia mientras cava y se apoya contra el sustrato (Salton y Sargis 2009). Si bien la profundidad de la rodilla brinda información sobre la ventaja mecánica de los músculos y sus comportamientos locomotores, su asociación con la preferencia de sustrato al menos para estos roedores y otros histricognatos, requiere una mayor revisión (Candela y Picasso 2008).

Otra condición que se relaciona con los hábitos locomotores es la asimetría de los cóndilos, siendo en las formas terrestres el cóndilo lateral más ancho que el medial (Argot 2002; Sargis 2002b; Candela y Picasso 2008), condición observada en *Spalacopus* y el resto de los octodóntidos (Pérez 2019). Además, la extensión distal de los cóndilos a la misma altura podría indicar una baja capacidad de aducción del fémur, como se observó en algunos roedores histricomorfos terrestres tales como *Dolichotis*, *Lagostomus*, *Dasyprocta* (Candela y Picasso 2008) y dentro de octodóntidos sólo en *Spalacopus*. Es importante destacar que la morfología de la epífisis distal femoral estaría más relacionada a la actividad (lenta vs. rápida) que al tipo de locomoción (terrestre *vs*. arborícola; ver Muizon y Argot 2003).

Tibia y fíbula. La tibia sigmoidea y levemente más larga que el fémur son condiciones descriptas como una morfología generalizada (Szalay y Sargis 2001; Argot 2002; Candela y Picasso 2008; Salton y Sargis 2009; Carrizo 2011). Este patrón se describe para *S. cyanus* y demás octodóntidos, aunque sólo en esta especie el espacio entre la tibia y la fíbula es mayor debido a una curvatura más evidente de la tibia, esto proporciona mayor superficie para el músculo *flexor digitorum fibularis* (ver Flores y Díaz 2009). Esto último fue descrito para marsupiales arborícolas, y en el caso de estos roedores no está muy clara su función; de acuerdo a Szalay y Sargis (2001) no es probable que estas características sean indicativo confiable de los atributos funcionales que se pueden vincular a las condiciones ecológicas, particularmente la preferencia de sustratos o modos locomotores. Existen diversas teorías acerca de la curvatura de los huesos largos como la tibia, pero todas difíciles de entender como resultados de un equilibrio entre fuerzas femorocrurales, ya que tanto la presencia como ausencia de curvatura en la tibia se observa en mamíferos terrestres, escansoriales y arborícolas (Szalay y Sargis 2001).

Los cóndilos tibiales son asimétricos en *Splacopus*, el lateral más grande y más cóncavo que el medial, dicha asimetría les confiere mayor estabilidad en la articulación; este patrón morfológico fue observado en marsupiales terrestres y arborícolas, como en otros roedores histricognatos (Candela y Picasso 2008; Flores y Díaz 2009; Pérez 2019).

El *M. quadriceps femoris* se inserta directamente en la rótula, que a su vez se une a la tuberosidad tibial por el ligamento patelar y, por lo tanto, la tuberosidad tibial que se proyecta anteriormente aumenta la ventaja mecánica de este grupo muscular y permite una rápida extensión de la rodilla (Candela y Picasso 2008; Salton y Sargis 2009). Este desarrollo de la tuberosidad tibial se observa en formas terrestres de marsupiales y roedores (Szalay y Sargis 2001; Argot 2002; Candela y Picasso 2008; Flores y Díaz 2009; Carrizo 2011). En *Spalacopus*, al igual que los restantes octodóntidos, se observa una proyección anterior de la tuberosidad tibial. El conocimiento respecto a la variación de la forma de la tuberosidad tibial dentro del grupo de roedores histricognatos es escaso, algunos autores sostienen que es necesario estudiar en detalle la posible asociación con las habilidades cursoriales, cavadoras y saltadoras (Candela y Picasso 2008).

En la región distal de la tibia de *Spalacopus* y el resto de los octodóntidos (Pérez 2019), se observa que la superficie articular de la tibia para la tróclea astragalar está más extendida medio-lateralmente que antero-posteriormente lo que le otorga cierta movilidad a la articulación (Candela y Picasso 2008). Aunque, en coincidencia con marsupiales y otros histricognatos terrestres, los movimientos laterales estarían restringidos debido a que la superficie articular de la tibia presenta una faceta lateral cóncava separada de la faceta medial por una cresta más o menos evidente (Argot 2002; Candela y Picasso 2008).

La fíbula, es una estructura muy reducida no sólo en *Spalacopus* sino que en todos los miembros de Octodontidae, siendo una estructura muy sencilla con el extremo proximal en forma de abanico, características asociadas a una locomoción terrestre (Szalay y Sargis 2001; Argot 2002; Pérez 2019). Debido a que su función se limita a la transmisión de cargas compresivas longitudinales, su estructura delgada no es un inconveniente (Argot 2002). Además, la diáfisis de la fíbula no se curva ni es robusta por lo tanto los músculos que allí se originan, como el *flexor digitorum fibularis*, están reducidos y en consecuencia su función prensil, extensión y flexión del pie (Argot 2002; Flores y Díaz 2009; Carrizo 2011).

La mayoría de los roedores subterráneos usan el miembro posterior para sostener su cuerpo dentro de las madrigueras, mover el cuerpo hacia adelante, arrojar los desechos hacia atrás, retroceder en las madrigueras, entre otras actividades (Stein 2000). La unión de la tibia y fíbula genera una estructura más reforzada para desarrollar las actividades antes mencionadas, pero es importante destacar que este carácter por sí mismo no es un indicativo de un estilo de vida subterráneo (Stein 2000).

Para concluir, la morfología del postcráneo de *Spalacopus cyanus* exhibe características consistentes con algunas habilidades para excavar en determinados elementos, y otras con habilidades claramente coherentes con el hábito epigeo. Si bien la morfología funcional del postcráneo se está analizando en otros órdenes de mamíferos, incluso otros grupos de roedores, las descripciones detalladas y sus interpretaciones funcionales permanecen inconclusas para gran parte del orden Rodentia. Esta información permitiría mejorar las interpretaciones de adaptación morfológica para determinados movimientos en relación a la diversidad de hábitos locomotores como también cambios en la postura. Por otro lado, también se podrían ampliar las explicaciones a un contexto filogenético en busca de convergencias o apomorfías que permitan enriquecer los estudios de historia evolutiva tanto de representantes actuales como fósiles. En el caso particular de *Spalacopus* resulta interesante dilucidar el camino que esta especie tuvo hacia la vida subterránea, ampliando la información disponible de estos animales poco estudiados y enriqueciendo comparaciones con otros roedores tanto emparentados como de linajes más distantes. En referencia a lo anteriormente mencionado, la comparación con *Ctenomys*, roedor subterráneo y emparentado con octodóntidos, podría aportar resultados interesantes, más aún cuando la descripción de la morfología de sus elementos postcraneales es muy escasa y hasta nula si se considera el esqueleto axial.

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The fate of small-mammal carrion is affected by carcass size and visual conspicuousness in a Neotropical rainforest

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Scavenging of carrion is essential to terrestrial ecosystems and can shape food webs and behavior. The prevalence and importance of scavenging has often been underestimated and overlooked in food web studies. Small-mammal carrion is even less studied and difficult to estimate, especially in the Neotropics. This project explored small-mammal carcass scavenging in a Neotropical, mid-elevation rainforest, and specifically studied the rate of carcass removal by scavengers, how the conspicuousness and weight of carcasses affect scavenging, and what vertebrate scavengers utilize this carrion resource. I deployed 194 mouse carcasses of various weights, above and below the leaf litter, and surveyed them daily until disappearance. I paired each carcass with a trail camera to help identify vertebrate scavengers. A general linear model analysis showed that most mouse carcasses disappeared within 1 to 2 days. Carcasses above the leaf litter were removed quicker and larger mice generally lasted longer. Only 6.25 % of the carcasses were removed by vertebrates. Most carcasses were removed by something too small to trigger the trail cameras, likely scarab beetles. The results of this study show that small-mammal carcasses are a sought-after resource in Neotropical forests, and that invertebrates are able to quickly hoard and secure small carrion more efficiently than vertebrate scavengers. A better understanding of scavenging ecology in Neotropical forests will help in developing a broader framework of the trophic interactions within and across ecosystems.

El consumo de carroña es esencial en los ecosistemas terrestres e influye en la estructura de redes tróficas, así como la conducta animal. A pesar de eso, este es un aspecto poco estudiado en los estudios de redes alimentarias. El papel que juega la carroña de mamíferos pequeños ha sido aún menos estudiada y muy difícil de estimar, especialmente en el Neotrópico. En este estudio investigamos la recolección de carroña por parte de pequeños mamíferos en un bosque lluvioso neotropical de elevación media. Estudiamos específicamente la tasa de recogida de cadáveres por parte de los carroñeros, así como lo conspicuo y el peso de la carroña y como esos factores afectan su recolección, y qué recolectores de vertebrados utilizan la carroña. Con tal fin se colocaron 194 carroñas de ratones de peso variado, tanto encima como debajo de la hojarasca, y se examinaron diariamente hasta su desaparición. Se colocó una cámara video apuntando a cada carroña para ayudar a identificar los carroñeros de los vertebrados. Un análisis general de tipo lineal mostró que la mayoría de la carroña de ratones desaparecieron entre 1 y 2 días. La carroña por encima de la hojarasca se consumió más rápido y la carroña de mayor tamaño generalmente duró más. Sólo el 6.25 % de la carroña fue removida por vertebrados. La mayoría de la carroña fue removida por agentes demasiado pequeños para activar las cámaras y sospechamos que esos agentes eran escarabajos. Los resultados de este estudio sugieren que la carroña de mamíferos pequeños son un recurso esencial en los bosques neotropicales, y que los invertebrados pueden acumular y renovar rápidamente carroña pequeña de manera más eficiente que los vertebrados carroñeros. Una mejor comprensión de la ecología del carroñerismo en los bosques neotropicales ayudará a desarrollar un marco más amplio de las interacciones tróficas dentro y entre los ecosistemas.

Keywords: *Canis latrans*; *Coprophanaeus; Didelphis marsupialis*; *Eira barbara*; food web; leaf litter; *Nasua narica*; *Philander opossum*; rainforest; scarabaeidae.

Introduction

Scavenging is a mode of feeding in which organisms acquire nutrients from carrion. Obligate scavengers, such as vultures, rely entirely on carrion as a food resource, whereas facultative scavengers acquire some, but not all of their nutritional needs from carrion. Scavenging is phylogenetically widespread in vertebrates and invertebrates, and plays an essential role in terrestrial ecosystems. For instance, this mode of feeding is crucial for the recycling of energy and matter in food webs, and for accelerating nutrient cycling and widely distributing these nutrients across the landscape (Putman 1978; Braack 1987; DeVault *et al.* 2003; Selva and Fortuna 2007; Parmenter and MacMahon 2009; Barton *et al.* 2013). In addition, scavenging can have extensive consequences for the shape and stability of food webs (Wilson and Wolkovich 2011; Beasley *et al.* 2015), and have far-reaching effects on organisms and populations, including shaping the evolution of behavior, social systems, and inter- and intra-specific interactions (Cooper 1991; Shivik 2006; Krofel *et al.* 2012; Moleón *et al.* 2014; Allen *et al.* 2015).

Due to its nutrient-rich, yet spatially and temporally patchy distribution, carrion is a unique resource that can have important effects on soils (Bump *et al.* 2009), microbes (Yang 2004), plants (Towne 2000; Bump *et al.* 2009), trophic webs (Barton *et al.* 2013), nutrient cycling and species diversity (Hocking and Reynolds 2011; Olson *et al.* 2012; Barton *et al.* 2013). Large and small-scale habitat differences can affect the fate of carrion, and ultimately its availability for, and monopolization by scavengers (DeVault and Rhodes 2002; DeVault *et al.* 2004; DeVault *et al.* 2011; Turner *et al.* 2017; Pardo-Barquín *et al.* 2019;

Stiegler *et al.* 2020). For example, Houston (1985) found that carrion persisted longer for vertebrate scavengers in Neotropical rainforests compared to Afrotropical forests. Factors such as temperature, humidity, rainfall, season, and the composition of the insect community can affect the rates at which decomposers utilize carcasses (Houston 1985; DeVault *et al.* 2003; Selva *et al.* 2005; Selva and Fortuna 2007), and thus the availability of this food source to scavengers (DeVault *et al.* 2003).

Carrion availability can vary greatly within and across terrestrial ecosystems, and depends on the cause of mortality and the accessibility of the carcass location (Moleón *et al.* 2019). Empirical data showcasing the prevalence of carrion biomass in different ecosystems are scarce (DeVault *et al.* 2003; Barton *et al.* 2019; Moleón *et al.* 2019). The proportion of mortality due to predation versus other causes probably results in an important amount of food for scavengers, making it likely that more energy is transferred through scavenging than predation in trophic webs (Wilson and Wolkovich 2011). The percentage of animal deaths due to causes other than predation is thought to be fairly high in many ecosystems: >95 % of reindeer deaths in northern Scandinavia (Tyler and Øristland 1995), 25 to 88 % for large mammals in a Polish forest (Jedrzejewski *et al.* 1993), ~70 % for large ungulates in the African savannah (Houston 1979).

However, the availability and utilization of small-mammal carcasses is inherently more difficult to determine. Due to their size, small-mammal carrion can be consumed entirely by a scavenger and disappear more quickly. Small-mammal carrion may be more difficult to detect (by scavengers or researchers), especially in a structurally-complex habitat. Some estimates calculate that ~40 % of small-mammal mortality is made available to scavengers and decomposers (Akopyan (1953) as referenced by Putman (1976) and DeVault *et al.* (2003). Oksanen *et al.* (1997) showed 83 to 98 % of small-mammal deaths in the Arctic were not due to predation. Undoubtedly, the large reproductive output of most small mammals likely provides a large number of carcasses (Cowles and Phelan 1958). However, this does not show the importance of the energetic link between small-mammal populations to the scavenger community.

Even though scavenging is a widespread and important ecological process, it is poorly understood, underestimated, or overlooked in food web models (Wilson and Wolkovich 2011; Barton *et al.* 2013, Moleón *et al.* 2014), stemming in part by the difficulty in quantifying carrion in ecosystems (Barton *et al.* 2019; Moleón *et al.* 2020). Additionally, the role of scavenging in ecosystems has been oversimplified, with facultative scavenging often categorized as random or opportunistic, although research is now showing highly nested patterns and complex interactions dictating scavenger community structure (Selva and Fortuna 2007; Olson *et al.* 2016). In particular, we lack a comprehensive understanding of the fundamental role of scavenging in various ecosystems (Beasley *et al.* 2019), and the factors that shape and structure scavenging communities and scavenger behavior (DeVault *et al.* 2003; Wilson and Wolkovich 2011; Barton *et al.* 2013). For instance, despite facultative scavengers being more common than obligate scavengers, they are neglected in trophic studies. This is due, in part, to facultative scavengers described typically as predators or omnivores, and their roles as scavengers being unknown or ignored (Wilson and Wolkovich 2011). Scavenging by vertebrates is underestimated (Wilson and Wolkovich 2011; Barton *et al.* 2013), as scavenging research has often focused on arthropod scavenging (Barton *et al.* 2013). Additionally, research on understanding the species diversity and composition of the scavenger communities is timely, as they have been negatively affected by global change (Olson *et al.* 2012; Beasley *et al.* 2015; Buechley and Şekercioğlu 2016), and anthropogenic influences can drive changes in scavenger assemblages (Sebastián-González *et al.* 2019; Sebastián-González *et al.* 2020). Therefore, in order to better model food web dynamics, understand the intricate ecology of terrestrial ecosystems, and restore ecosystem services, it is important for scavenging to be quantified, and for scavengers to be identified.

Studies focused on elucidating the role and patterns of scavenging in Neotropical ecosystems are also lacking (Beasley *et al.* 2019; Sebastián-González *et al.* 2019). This is particularly true for understanding the dynamics and contribution of vertebrate scavengers and small-mammal carrion in these complex ecosystems. Studies that investigate scavenging in the Neotropics have focused mostly on arthropods or vultures, or have detailed scavenging observations of single species (Houston 1985; Houston 1986; Houston 1988; Lemon 1991; Gomez *et al.* 1994; O'Donnell 1995; Villegas-Patraca *et al.* 2012; Mallon *et al.* 2013; dos Santos *et al.* 2014; Arroyo-Arce *et al.* 2016; Ucha and Santos 2017; Romero *et al.* 2020). Scavenging is thought to be significant in Neotropical forests. Houston (1986) estimated in Barro Colorado Island, Panama, that 4.1 kg/km^2 of mammals die every day. This amount surpasses those calculated for Afrotropical forests: 4.3 times higher than Lombe Forest, Cameroon and 1.58 times higher than Kibale Forest, Uganda (Houston 1985). Even though some proportion of these deaths is due to predation (Houston 1985) a large amount of carcasses would be made directly available to the scavenger community.

The goals of this project are to understand the importance of small-mammal carrion, scavenging, and factors that affect scavenging rates in a mid-elevation Neotropical rainforest. Specifically, I aim to study: 1) What are the rates of small-mammal carcass removal? 2) How does visual conspicuousness (position in the leaf litter) and size of the carcass affect scavenging rate? 3) What vertebrates are involved in scavenging the small-mammal carcasses? I use an experimental approach to explore these questions by placing fresh rodent carcasses above and below the leaf litter, along with trail cameras. This project provides insight into the importance of small-mammal carrion as part of the food-web dynamics of mid-elevation tropical rainforests.

Materials and methods

I conducted this study in Las Brisas Nature Reserve (10.0670°, -83.6376°), Limón province, Costa Rica. Las Brisas is situated in the northeastern slopes of the Volcán Turrialba, within the central volcanic range of Costa Rica. The elevation in the reserve is 650 – 1,030 m above sea level, situating it as a mid-elevation forest. Las Brisas is composed of a mixture of old growth and secondary forests of various stages, along with some scrub and open areas. The reserve is located on a continuous range from the Caribbean lowlands to the highlands of Volcán Turrialba (https://www.lasbrisasreserve.com/aboutus). Access to the reserve is limited because it is privately owned and maintained, and although there is a system of trails, human presence is relatively limited.

To assess scavenging rates I set out and surveyed 194 mouse carcasses (*Mus musculus*) within the forested area of the Las Brisas Nature Reserve from 29 May through 8 June 2018. I purchased commercially available euthanized and frozen feeder mice (mouse meals for pets such as snakes) from a local supplier. Mouse carcasses were thawed at room temperature approximately 1 to 2 hours prior to placement in the field. I handled all carcasses with latex gloves, and weighed the thawed carcasses before deploying them. The average carcass weight was 11.64 g (*n* = 194; SE = 0.40; SD = 5.55; median = 10.5). The weight ranged from 3.4 to 25.8 g. The carcasses had white pelage, which was the only mouse color available from the supplier, but also mimics the ventral pelage of several species found in these Costa Rican forests.

I placed the carcasses ventral side up in areas that were accessible by the trail system in Las Brisas. Carcasses were placed at a minimum of 50 m from each other, 0 to 5 m off the trails. To test how visual conspicuousness affects scavenging rates, I placed 98 carcasses on top of the leaf litter and 96 below the leaf litter. To conceal the carcasses below the leaf litter, I moved fallen leaves with a stick, placed the carcass on the ground and covered it fully with the displaced leaves. After deploying the carcasses, I surveyed them daily until they had disappeared or had decomposed past the point of having any flesh remaining, which is how I determined carcass removal time (days elapsed since carcass deployment) since trail cameras are not triggered by invertebrates.

In addition to the daily sampling, I also placed trail cameras on each deployed mouse carcass to document scavengers. I used Ltl Acorn 5210-A (Guangdong, China) and Foxelli Outdoor Gear Oak's Eye Trail Camera (Vlaardingen, The Netherlands), on the most sensitive triggering settings, to record video for 30 seconds with no lapse time between videos. Trail cameras were set to trigger based on motion. The cameras were placed on existing structures within the forest a few meters away from the deployed carcass to identify scavengers. Although I attempted to set a camera on each deployed carcass, human error or equipment malfunction allowed me to get video recordings from 160 deployments. When reviewing the videos, I was conservative when identifying scavengers; animals were only categorized as scavengers if they were seen grabbing or consuming the carcass on the video.

Throughout the project I noticed that small mounds appeared where many carcasses had been deployed, and it was not until later in the experiment that I realized that something too small to be picked up by the trail cameras was burying the mouse carcasses. To investigate what was doing this, I dug below a few of the mounds and was able to follow narrow tunnels to my deployed carcasses buried ~15 to 20cm deep. Attached to one of the buried mice were two *Coprophanaeus corythus* (Scarabaeidae) beetles. Unfortunately, I did not start recording data on whether beetles were burying the carcasses until too late into the study, but a large proportion of my carcass deployments exhibited the unique dirt mounds.

I used a general linear model to test the effect of weight (continuous independent variable) and position on the leaf litter (categorical independent variable - above or below) on carcass removal time (dependent variable – transformed data on days elapsed since carcass deployment). I transformed the dependent variable of days elapsed since deployment to eliminate heteroskedasticity by taking the natural logarithm of the values plus one. I calculated carrion consumption rate, a measure of carrion biomass consumed divided by consumption time (g/hr), for carcasses in the two leaf litter treatments (above and below), and all data combined. I used MiniTab v. 18 for all statistical analyses. This study was approved by the University of Wisconsin's IACUC committee and Las Brisas Nature Reserve management, and permits were issued by Costa Rica's government agency MINAE.

Results

Scavengers removed the majority of mouse carcasses throughout the study. Of 194 carcasses placed in the forest, 193 (99.48 %) were removed by vertebrate or invertebrate scavengers, and only one was fully consumed by decomposers. Although I did not quantify the efficiency of beetles in burying carcasses, their ubiquitous mounds suggest they were dominant in monopolizing this resource. Only one carcass, placed below the leaf litter, decomposed and left behind remains of fur and bones six days after deployment. When all data are pooled together, the average number of days for carcass removal by scavengers is 1.57 days (SE = 0.05; SD = 0.71; median = 1). Over half (54.12 %) of the mouse carcasses were removed within 24 hours, and 90.21 % of carcasses were removed within 48 hours (Figure 1). The average consumption rate was higher for carcasses placed above ground (0.396 g/hr; SE = 0.022; SD = 0.221) than those placed below the leaf litter (0.306 g/hr; SE = 0.017; SD = 0.174); overall carrion consumption rate was 0.352 g/hr (SE = 0.014; SD = 0.204).

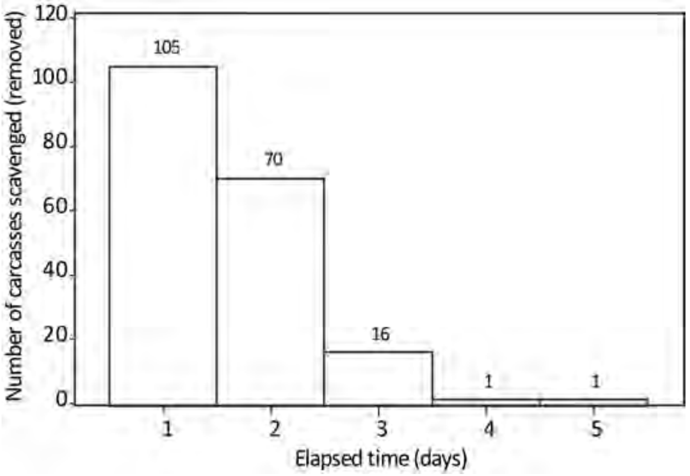

Figure 1. Histogram of number of carcasses removed by days after carcass deployment using all data pooled together.

The general linear model, with time to carcass removal as the dependent variable, shows a significant difference for both independent variables: weight (*n* = 194; F = 8.67; *P* = 0.004), and position on the leaf litter (*n* = 194; F = 19.58; *P* < 0.001; Figure 2). The model summary shows an R-squared of 12.77 %. Weight had a small significant effect (regression slope for above and below leaf litter = 0.01521) resulting in larger carcasses lasting slightly longer. Overall, the carcasses placed above the leaf litter are removed more quickly than those below the leaf litter. The average number of days until the removal of a carcass placed above the leaf litter is 1.35 days (*n* = 97; SE = 0.06; SD = 0.63; median = 1). For these carcasses, 70.1 % were removed by 24 hours, and 96.9 % by 48 hours (Figure 3). The maximum number of days before a scavenging event for carcasses above the leaf litter is five days. In contrast, the average number of days until the removal of a carcass placed below the leaf litter is 1.78 days (*n* = 96, SE = 0.07; SD = 0.73; median = 2). Removal rate for carcasses placed below the leaf litter is 38.5 % within 24 hours, and 83.5 % within 48 hours. The maximum number of days before scavenging for carcasses under the leaf litter is 4 (Figure 4). The regression equation for carcasses placed above the leaf litter is Ln (days until removal + 1) = 0.0631 + 0.01521 × weight. The regression equation for carcasses placed below the leaf litter is Ln (days until removal + 1) = 0.3163 + 0.01521 × weight.

Out of the videos captured on 160 carcass deployments, 10 videos showed a scavenging event by a vertebrate (6.25 %). The most common vertebrate scavenger recorded was the common opossum (*Didelphis marsupialis*), followed by gray four-eyed opossum (*Philander opossum*) and coyote (*Canis latrans*). Four videos showed a Russet-naped Wood-Rail (*Aramides albiventris*) pecking at carcasses, but not consuming the entire carcass. In five videos a variety of ver-

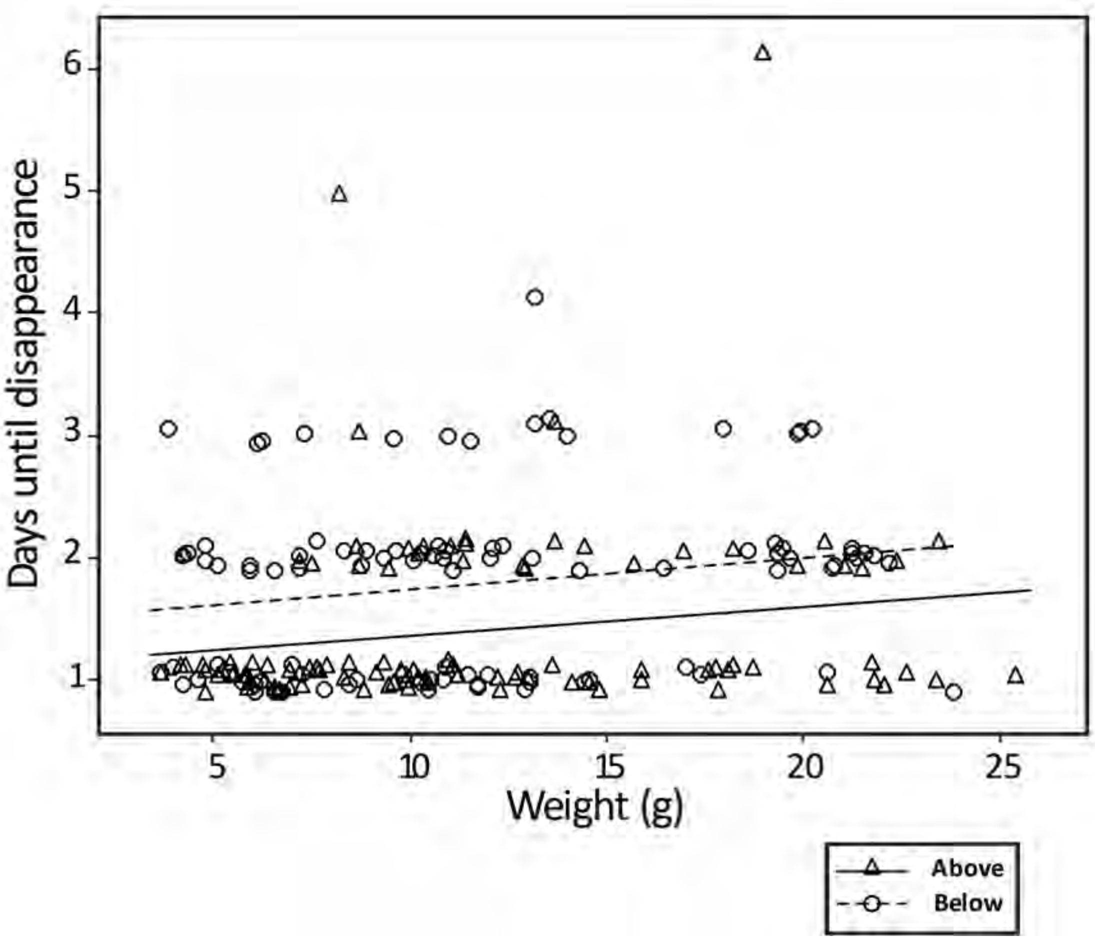

Figure 2. Scatterplot (with regression and position in the leaf litter) of days until disappearance (how long it took for a scavenger to remove the carcass) vs. weight of mouse carcass.

Figure 3. Interval plot of days until disappearance (how long it took for a scavenger to remove the carcass) vs. location in the leaf litter. Dot represents the mean. Error bars are one standard error.

tebrates are seen exploring and sniffing intently the area where the carcass was located, or had been located prior to disappearance. These videos showed tayras (*Eira barbara*), coatis (*Nasua narica*), and Russet-naped Wood-Rails interacting with the carcass or sniffing and searching where the carcass had been deployed (Table 1).

Discussion

Small-mammal carcasses were removed very quickly in this study (1.57 days on average), and only one carcass decomposed in place. The proportion of carcasses removed in the first days, show that carrion is an important and sought-after resource in these Neotropical rainforests. Indeed, the time to carcass removal was assuredly overestimated since the presence/absence of the carcass was determined via surveys that were only conducted every 24 hours. The speed at which carrion is monopolized can vary by habitat type and ecosystems (Beasley *et al.* 2015); studies in temperate regions show a wide range of carcass disappearance speed for small-mammal carrion, but are typically longer than that reported here: 2.58, 5.6, and 1.23–3.30 days (DeVault and Rhodes 2002; DeVault *et al.* 2004; Olson *et al.* 2012). Research done in the Neotropics with domestic chickens found a quick carcass removal time of ~10 hours (Houston 1986; Houston 1988). Temperature and humidity in the tropics likely create conditions in which microbes colonize carcasses quickly, and olfactory cues that can alert scavengers of carrion are emitted more quickly. Competition between a wide range of scavengers and decomposers is seemingly high.

One of the most striking aspects of this study is the relatively few instances of recorded scavenging by vertebrates. My study's rate of efficiency by vertebrate scavengers (6.25 %) is much lower than those reported in the literature. Although differences exist based on the location of the study, and the type and size of carcass used, published estimates of vertebrate scavenging efficiency in terrestrial habitats averages ~75 %, and ranges from 13 % to 100 % (DeVault *et al.* 2003). If we focus on research that only utilizes small mammals as carrion bait, vertebrates are also the dominant scavengers, ranging in efficiency from 35 % to 100 % (Mullen and Pitelka 1972; DeVault and Rhodes 2002;

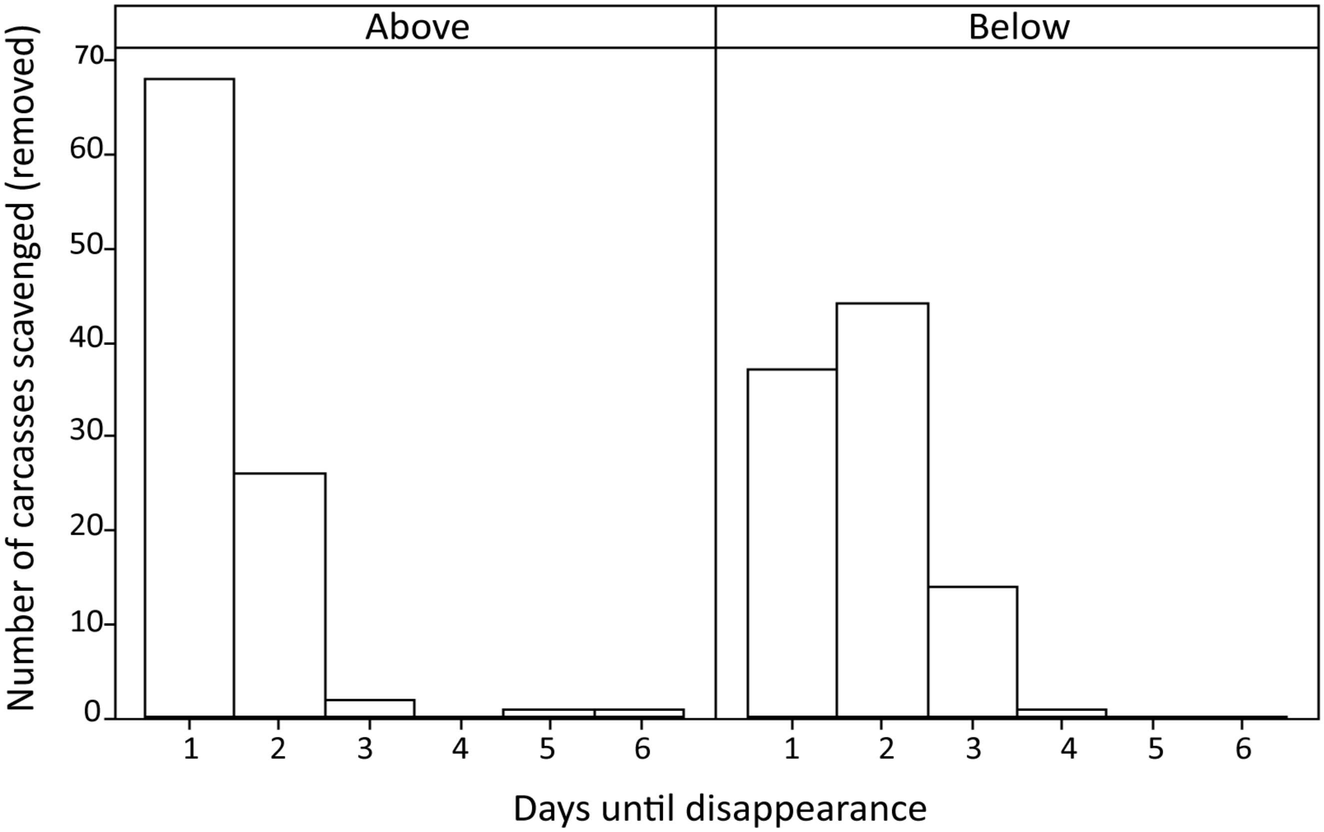

Figure 4. Histograms of number of carcasses removed by days after carcass deployment for above and below the leaf litter.

Table 1. Vertebrate scavengers and their activity at carcass location.

Common name	Species	Number seen	Interaction with carcass
Common opossum	*Didelphis marsupialis*	6	Scavenging
Russet-naped Wood-Rail	*Aramides albiventris*	4	Pecking at carcass, but not consuming or removing it
White-nosed coati	*Nasua narica*	3	Sniffing near carcass or where carcass had been located
Coyote	*Canis latrans*	2	Scavenging
Gray four-eyed opossum	*Philander opossum*	2	Scavenging
Tayra	*Eira barbara*	2	Sniffing near carcass or where carcass had been located

DeVault *et al.* 2003; DeVault *et al.* 2004; DeVault *et al.* 2011; Turner *et al.* 2017). Given the large number of deployments that had working trail cameras during pickup, equipment malfunction is unlikely to be the reason why we see this trend. It is, however, probable that the small-mammal carcasses were consumed or removed by invertebrates too small to activate the camera.

Invertebrate scavengers can consume high proportions of carcasses compared to vertebrates (Cornaby 1974; Ray 2014), and beetles were likely a strong force in the removal of whole carcasses during this study. Although I did not quantify the removal of carcasses by beetles from the start of the study, I did notice many conspicuous mounds in the carcass deployment locations. Similar research in a Costa Rican lowland forest showed that ~70 % of small-mammal carcasses deployed on the ground were removed by beetles (Romero, unpublished data).

The results of this study pertaining to carcass weight are also probably a function of the interaction between the beetles and the carcasses rather than the vertebrate scavengers. We know that for the biomass of small-mammal carcasses, *Coprophanaeus* beetles are more effective in quickly locating and hoarding this resource. Given the regression equations, the smallest deployed mouse (3.4 g) would have been consumed or buried on average 8.18 hours quicker than the largest mouse (25.8 g). Very little ecological and behavioral information is available for these beetles (Edmonds 2010), and it is not known how long they take to bury a mouse carcass. The *Coprophanaeus corythus* beetles I found were very small (~25 mm), so it is not hard to imagine that larger carrion would generally take longer to bury. At some point carcass size would become limiting to the beetles' ability to bury and exploit carrion. There must be a threshold at which these beetles no longer bury carcasses, and vertebrate scavenging may become more dominant, which may result in carrion partitioning, a pattern documented in other scavenging systems (see Moleón *et al.* 2017; Muñoz-Lozano *et al.* 2019).

How scavengers detect and locate carrion may be critical to understanding how this system of scavengers is maintained. Some research supports the idea that visual conspicuousness is important for scavengers to locate carrion (Selva *et al.* 2005). Olfactory cues, however, may be more important in attracting a suite of vertebrate scavengers to carcasses (Houston 1986; DeVault and Rhodes 2002; Potier *et al.* 2019). DeVault and Rhodes (2002) did not find a significant difference in the rates of scavenging on carcasses placed above and below leaf litter. Houston (1986) found that Neotropical vultures were able to locate the general area where chicken carcasses had been deployed above and below the leaf litter, and vultures were able to consume these carcasses within hours regardless of their leaf-litter position. My study found a difference in the time to removal of carcasses placed above and below the leaf litter, although the proportion of carcasses removed by scavengers (compared to entirely decomposing) was almost 100 % for both. In addition, it is important to note that while carcass time to removal was significantly different for those placed above and below the leaf litter, carrion in both categories were scavenged relatively quickly, and the difference equated, on average, to only a matter of hours (above = 1.35 days, below = 1.78 days). This result may be due to microhabitat differences in relation to temperature, humidity, and exposure to direct sunlight (Sayer 2006), which affects the rate at which carcasses decompose and emit odor (Putman 1978; Shean *et al.* 1993). As DeVault and Rhodes (2002) note, olfactory cues are likely important for mammalian scavengers; and both their study and mine recorded mammals sniffing in areas where carcasses had been placed but had already disappeared.

This study highlights the importance of small-mammal carrion as a sought-after resource in Neotropical rainforests. Carcass consumption rate may seem low (*cf.* Sebastián-González *et al.* 2016; Gutiérrez-Cánovas *et al.* 2020; Sebastián-González *et al.* 2020), but is most likely a function of the small carcass size. The speed at which small-mammal carcasses are entirely consumed or hoarded by scavengers is extremely fast. The relatively low rate of vertebrate scavenger efficiency in exploiting small-mammal carrion makes this ecosystem particularly unique. Further research should explore why beetles are seemingly outcompeting vertebrates. They may be locating these carcasses faster, detecting putrifaction cues at lower concentrations, or are simply highly abundant and able to arrive at the carcasses more quickly. While the efficiency of different scavenger guilds (vertebrates vs. beetles) can vary in different habitats, ecosystem function is typically sustained (Sugiura *et al.* 2013; Sugiura and Hayashi 2018). Therefore, research focused on understanding how these complex interactions between invertebrate and vertebrate scavengers maintain ecosystem function would be timely to help create a more developed framework for Neotropical food webs.

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Contribution of camera-trapping to the knowledge of *Abrocoma boliviensis*

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Rare and endemic rodent species, such as the critically endangered Bolivian chinchilla rat, *Abrocoma boliviensis,* are infrequently captured using traditional trapping methods. Therefore, to determine their presence and abundance, indirect records (bird pellets, feces, bone remains) are often used. Although not a popular method for rodents, the incorporation of photography is known to provide precise data. Therefore, the objective of this report was to demonstrate the importance of using photographic records and occupancy models in the study of the distribution and ecology of a small-body species with high conservation value. We used photographic records obtained from 180 camera-trap nights in two areas of the Andean dry forests of Bolivia, during both wet and dry seasons. Data analysis include the estimates of presence probability of *A. boliviensis* in the study sites, using an exploratory occupancy analysis. The estimated presence probability of *Abrocoma boliviensis* for the study sites were 30.2 % during dry season and 33.9 % during wet season. However, due to the limited amount of photographic records for the species, it was not possible to accurately determine the factors affecting the species presence probability. Camera-trapping records and associated metadata provided new ecological and distribution data for the Bolivian chinchilla rat. In combination with information about threats that the species faces, our data may be useful in generating and applying conservation actions.

Roedores raros y endémicos como la críticamente amenazada rata chinchilla boliviana, *Abrocoma boliviensis*, son escasamente capturadas con el uso de trampas tradicionales. Contar con diferentes registros indirectos como egagrópilas, heces, restos de huesos y letrinas, aproximan a determinar la presencia de especies muy importantes. Los registros fotográficos, a pesar de no ser un método popularmente utilizado en roedores, se pueden considerar como datos precisos para el desarrollo de investigaciones. Por ello, el objetivo de este trabajo fue mostrar la utilidad de los registros fotográficos y modelos de ocupación en estudios sobre la distribución y ecología de especies de pequeño tamaño, pero con gran valor de conservación. Se utilizaron fotografías obtenidas a través de campañas de foto-trampeo durante 180 noches, en épocas seca y húmeda, en dos áreas de bosques secos andinos de Bolivia. Se analizó la probabilidad de presencia de *A. boliviensis* en el área de estudio a través de un análisis exploratorio mediante el uso de modelos de ocupación. Se determinó una probabilidad de presencia de la especie en el área de estudio del 30.2 % para la época seca y de 33.9 % para la húmeda. Debido a una limitada cantidad de registros fotográficos de *A. boliviensis*, no se pudo determinar con exactitud qué factores afectan la probabilidad de presencia de la especie. Los registros fotográficos obtenidos de foto-trampeo demostraron tener un potencial en las búsquedas de nuevas localidades donde reside la rata chinchilla boliviana. Esta nueva información obtenida acerca de especies únicas y elusivas como *A. boliviensis* aportan al conocimiento de su ecología, y por ende, derivan en la generación y aplicación de medidas para su protección y el de sus hábitats potenciales.

Keywords: Andean dry forests; Bolivian Chinchilla Rat; occupancy modeling; photographic records; rodents.

Introducción

Dentro de los mamíferos, los roedores constituyen uno de los grupos más diversos y menos conocido (Burgin *et al.* 2018); debido a su actividad nocturna, conducta elusiva y baja probabilidad de captura el conocimiento sobre su comportamiento es muy escaso (Tarifa *et al.* 2009; Ferreguetti *et al.* 2018a; Thomas *et al.* 2020) en particular de aquellas especies amenazadas, endémicas o raras (Úbeda *et al.* 1994; Pacheco 2002; Tarifa y Aguirre 2009; IISE 2011; Law *et al.* 2016). La rata chinchilla boliviana, *Abrocoma boliviensis* (Rodentia: familia Abrocomidae), es una especie endémica para Bolivia y está categorizada como "En peligro crítico" tanto a nivel nacional (Tarifa y Aguirre 2009) como internacional (Bernal 2016). Además, *A. boliviensis* es miembro de un grupo selecto de las 100 especies de mamíferos considerados con el más alto valor para la conservación por ser una especie evolutivamente distinta y globalmente amenazada (Isaac *et al.* 2007; EDGE 2019).

Bolivia presenta dos especies de Abrocomidae (Patton *et al.* 2015), *A. cinerea*, con amplia presencia en la región altiplánica de los Andes y *A. boliviensis*, considerada endémica de los Andes Centrales de Bolivia (Aguirre *et al.* 2009; Bernal 2016). *A. boliviensis* sólo se conoce a través de dos especímenes colectados en la localidad tipo, Comarapa, en 1926 y 1955 (Glanz y Anderson 1990), y posteriores esfuerzos para registrar a la especie en esta localidad resultaron fallidas (Glanz y Anderson 1990). En otras localidades de Bolivia se encontraron indicios de la presencia de la especie, a través de restos obtenidos en estómagos de serpientes y fotografías (Rivero *et al.* 2004; Tarifa *et al.* 2009; Quinteros-Muñoz 2015; Hidalgo-Cossio *et al.* 2016). En los registros fotográficos, la especie es fácilmente identificable debido a sus características morfológicas, como la cola larga y peluda (Patton *et al.* 2015; Taraborreli *et al.* 2015); sumado a su tamaño, hocico corto y ancho, orejas grandes y redondas con una ligera muesca, patas gruesas y notorias respecto a otros roedores cricétidos (Glanz y Anderson 1990; Emmons 1999; Braun y Mares 2002). Por tanto, el uso de trampas cámara promete ser ideal para trabajar con esta especie, que, debido a su timidez, no es comúnmente capturada por trampas de captura viva (De Bondi *et al.* 2010).

Las trampas cámara son una herramienta de investigación ampliamente utilizada (Nichols *et al.* 2011; Díaz-Pulido y Payán Garrido 2012; Rovero *et al.* 2013; Meek *et al.* 2014), debido a que perturban mínimamente el hábitat y al ser un método no invasivo, son ideales para el trabajo con especies amenazadas (Long *et al.* 2011; Trolliet *et al.* 2014). Este método también aporta información sobre la historia natural de las especies y las interacciones entre especies y el medio en el que habitan (Nyiramana *et al.* 2011; Sweitzer y Furnas 2016). El uso de las trampas cámara ha logrado importantes aportes al conocimiento científico sobre roedores, como ser la presencia, patrones de actividad y comportamiento de estos animales, la cual puede ser utilizadas como base científica en programas enfocados en su conservación (Yamada *et al.* 2010; Suzuki and Ando 2018; Rendall *et al.* 2014; McDonald *et al.* 2015; Figueroa-De-León *et al.* 2016; Hegerl *et al.* 2017).

Los datos obtenidos a través de foto-trampeo se pueden utilizar de múltiples maneras y pueden ayudar a entender varios aspectos de la ecología de las especies en estudio (O'Conell *et al.* 2011). Los modelos de ocupación son un ejemplo, a través de los cuales se puede inferir sobre la probabilidad de la presencia de la especie, abundancia relativa, determinar su uso de hábitat y poder definir su distribución potencial (MacKenzie *et al.* 2006; Carbone *et al.* 2002; Nichols *et al.* 2011; Díaz-Pulido y Payán Garrido 2012).

En Bolivia, el Programa para la Conservación de Grandes Carnívoros Andinos (PCCA), realizó campañas de foto-trampeo en bosques secos del centro y sur de Bolivia, pertenecientes a la ecoregión "Boliviana-Tucumana" (Navarro y Maldonado 2005). A pesar de ser carnívoros medianos y grandes el principal objeto de estudio del PCCA, las trampas cámara lograron registrar la actividad de un amplio espectro de especies, entre ellas a *A. boliviensis*. Por ello, los objetivos de este trabajo fueron: demostrar la utilidad de registros fotográficos para generar datos sobre especies raras y difícilmente observables, usando a la rata chinchilla boliviana como ejemplo, y explorar la potencialidad de la aplicación de modelos de ocupación para la generación de información sobre este roedor endémico y críticamente amenazado.

Materiales y Métodos

Área de estudio. El estudio se realizó en dos áreas de bosques secos, que siguiendo la clasificación propuesta por Navarro y Maldonado (2005) e Ibisch y Mérida (2003), pertenecen a la región "Boliviana-Tucumana" que se ubica en el centro y sur de Bolivia (Figura 1). El primer sitio de estudio está localizado en seis comunidades pertenecientes al municipio de San Lorenzo (-21° 11' S, -64° 27' O), ubicado al norte del departamento de Tarija. El segundo sitio de estudio corresponde al Área Natural de Manejo Integrado Municipal (ANMIM) "Lagarpampa –Mollepampa" (-18° 21' S, -64° 59' O), perteneciente al municipio de Aiquile al sur del departamento de Cochabamba.

Ambas áreas son zonas montañosas con rangos altitudinales de 1,000 hasta 2,500 msnm. La vegetación natural de estos bosques fue altamente modificada debido a la expansión de cultivos y la ganadería extensiva de ramoneo en libertad (Josse *et al.* 2009).

Análisis. Se utilizaron registros fotográficos obtenidos mediante campañas de foto-trampeo realizadas por el PCCA, por tanto, el diseño del estudio estuvo basado en la obtención de datos del oso andino (*Tremarctos ornatus*, Carnivora). Se colocaron 46 estaciones de foto-trampeo en el área de San Lorenzo, cubriendo un área de 289.15 km^2 y 15 en el ANMIM "Lagarpampa-Mollepampa", cubriendo un área de 112.75 km^2. La distancia entre estaciones fue 1.5 km como mínimo. Es muy común que los estudios que utilizan el foto-trampeo se enfoquen en una sola especie, ignorando una potencial base de datos rica en información científica (Edwards 2018; Mazzamuto 2019). Si bien el oso andino presenta requerimientos ecológicos muy diferentes a los de *A. boliviensis* consideramos que los datos obtenidos de esta especie en el muestreo cumplen con los supuestos para la utilización de modelos de ocupación. Los supuestos determinados por MacKenzie *et al.* (2006) incluyen: 1) que la población en estudio sea cerrada, es decir, que no presente migraciones, muertes o nacimientos. Por dicha razón, se utilizaron datos obtenidos durante tres meses en época seca (agosto a octubre) y tres meses durante la época húmeda (enero a marzo). 2) que la toma de datos sea independiente, esto se logra por la distancia mínima entre cámaras, ya que siendo el área de acción de las especies altamente dependiente de su masa corporal (Tucker *et al.* 2014), creemos virtualmente imposible estar considerando al mismo individuo en dos estaciones de foto-trampeo. 3) que toda heterogeneidad se puede modelar, este supuesto se cumple ya que ambas áreas de estudio pertenecen a la misma ecorregión, presentan características similares y se muestrearon durante la misma época. Por tanto, las diferencias son detectables y fueron consideradas como covariables. 4) que no existan falsas detecciones, lo cual es fácilmente logrado porque las características morfológicas de *A. boliviensis* son particulares de la especie, lo cual hace que se la identifique correctamente. Asimismo, los modelos de ocupación, al calcular una probabilidad de detección, reducen posibles

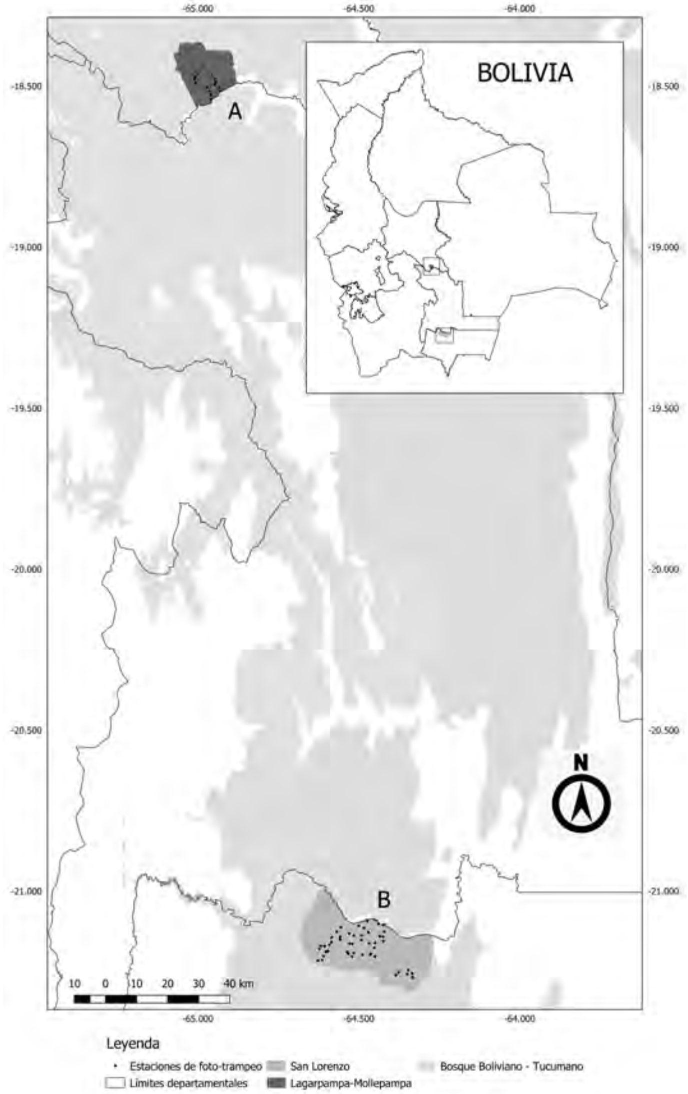

Figura 1. Mapa del área de estudio y localidad de las estaciones de foto-trampeo en Lagarpampa-Mollepampa, departamento de Cochabamba (A) y San Lorenzo, departamento de Tarija (B).

errores inducidos por la consideración de falsas ausencias, convirtiéndolos en una opción más atractiva frente a otras opciones de análisis (MacKenzie *et al.* 2006).

Una vez identificada la presencia de *A. boliviensis*, se verificaba la locación geográfica de la estación de foto-trampeo a la cual pertenecía la imagen, y el dato se incluía en una matriz de presencia-ausencia de la especie, llamada matriz de detección. Para realizar el análisis, se consideró una sola matriz de detección por época, la cual contenía las 61 estaciones de foto-trampeo como unidades de muestreo. Se procedió a un análisis exploratorio mediante el uso de modelos de ocupación a través del programa PRESENCE (v. 2.12.31; MacKenzie *et al.* 2006). Se escogieron cinco potenciales variables que se consideró podrían ser incorporadas en los modelos en este estudio, descritos a continuación:

Modelo de la trampa-cámara: se utilizaron dos tipos de cámaras diferentes, Cuddeback Ambush y Bushnell Trophy-Cam. Las que fueron colocadas de manera aleatoria en los diferentes sitios de muestreo, para ambas áreas consideradas. Debido a la sensibilidad, característica de cada modelo de cámara, se cree que ésta puede afectar la probabilidad de detectar especies de menor tamaño. Por tanto, se decidió utilizar el modelo como una variable de muestreo ya que potencialmente afecta la probabilidad de detección.

Hábitat alrededor de la cámara: considerando que los roedores tienen ámbitos de hogar reducidos, se consideró que el tipo de hábitat alrededor de la cámara es una variable que afectaría la probabilidad de presencia de la especie en el punto de muestreo. Se clasificó el hábitat de acuerdo a las características que ocupaban el 70 % de la fotografía, excluyendo el nivel del suelo. Por ejemplo, si la fotografía presentaba roquedales en la mayoría de los alrededores se clasificaba como hábitat rocoso.

Sustrato: se consideró importante separar el sustrato de la variable "hábitat", puesto que éste parece estar más afectado por el cambio de época y uso por otros animales. Se clasificó al sustrato de acuerdo a las características presentadas por al menos el 70 % del área cubierta por la fotografía a nivel del suelo. Por ejemplo, si el suelo en una fotografía presentaba mayormente helechos y otras plantas, se lo consideraba como un sustrato dominado por vegetación.

Elevación: en metros sobre el nivel del mar en el punto de muestreo.

Presencia de Leopardus geoffroyi: de acuerdo a lo observado en las fotografías analizadas, se observó que la presencia de esta especie y *A. boliviensis* parece estar fuertemente relacionada. Por tanto, si se encontraba al menos un registro fotográfico de este felino durante el periodo de muestreo para un sitio de muestreo, se lo consideraba como presente.

Resultados

Se obtuvieron 33 registros fotográficos en 14 estaciones para la época seca y 95 en 18 estaciones durante la época húmeda (Figura 2). La variación en elevación de dichos datos es 1,002 a 2,358 msnm. No existen registros previos de la presencia del género *Abrocoma* en la zona de estudio, por lo que nuestros datos son inéditos para el género. Las características morfológicas de los individuos fotografiados, cola larga y gruesa por ser peluda y las patas delanteras notorias además del tamaño en relación a otras especies y el tipo de hábitat, con roquedales abundantes y vegetación nativa, sugiere -sin lugar a dudas- de que los registros reportados en este trabajo corresponden a animales del género *Abrocoma* (Figura 2). Sobre la base de los bien conocidos patrones de distribución de otras especies del género y a las características morfológicas de los individuos fotografiados consideramos altamente confiable afirmar que estos animales corresponden a la especie *Abrocoma boliviensis*.

Con los datos obtenidos se procedió a construir modelos de ocupación, tres modelos para la época seca y tres modelos para la época húmeda (Tabla 1). Se dejó de considerar más modelos cuando éstos ya no convergieron y fueron ignorados en el análisis. Los resultados preliminares

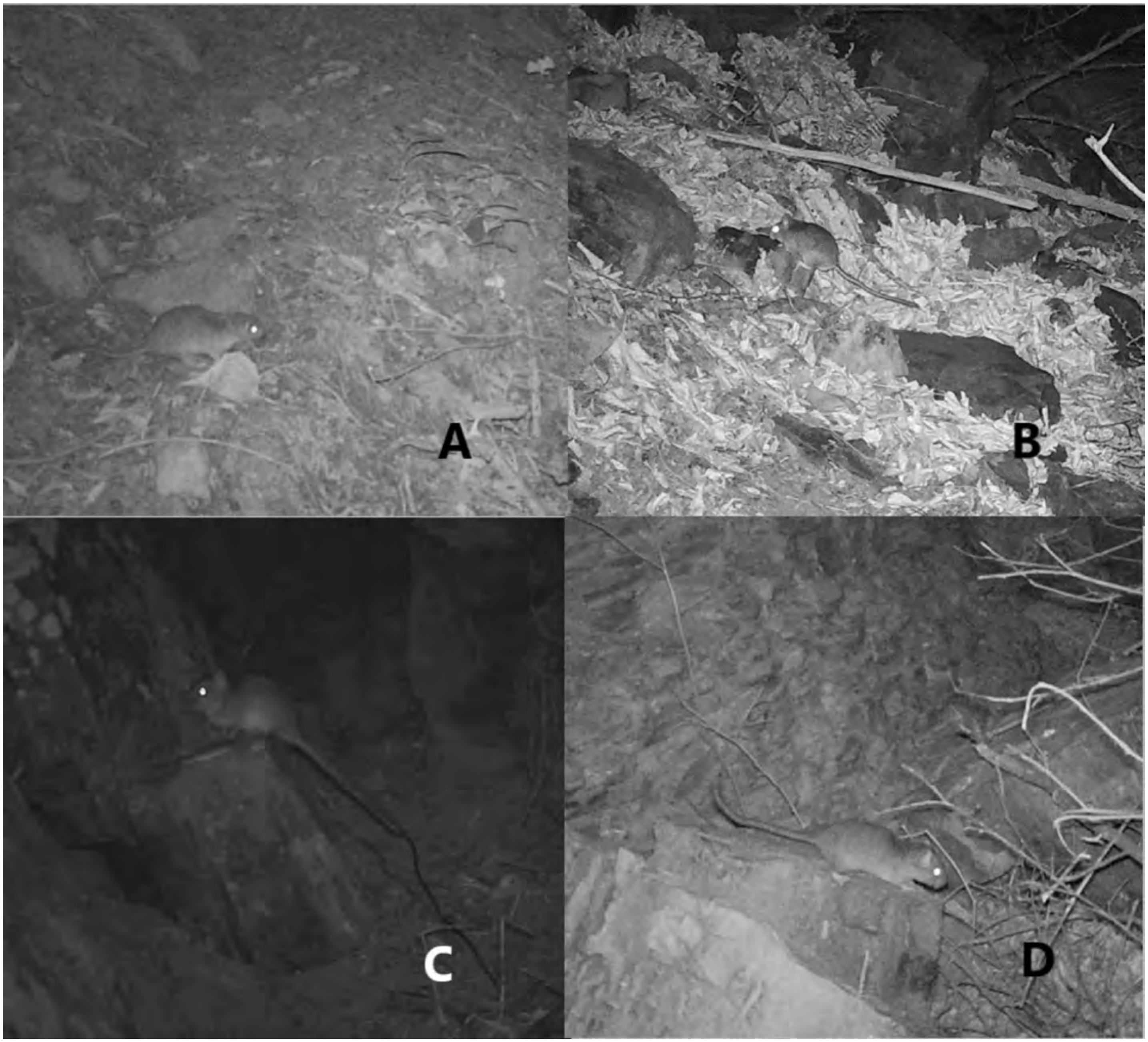

Figura 2. Registros de *Abrocoma boliviensis* en las trampas cámara. Donde (A) y (B) *A. boliviensis* se encuentra en un sustrato dominado por hojarasca, en la localidad de San Lorenzo y Lagarpampa-Mollepampa, respectivamente. Las figuras (C) y (D) muestran un sustrato dominantemente rocoso, en la localidad de San Lorenzo y Lagarpampa-Mollepampa, respectivamente.

determinan una probabilidad de ocupación ingenua (naïve occupancy) de 0.3023 para la época seca y 0.3396 para la época húmeda, las cuales nos sirve como base comparativa para demostrar las mejoras en los resultados obtenidos con una modelación integrando variables. Estos valores pueden ser interpretados como probabilidades de presencia de 30.23 % y 33.96 % de la especie en el área muestreada, comparable al 33 % obtenido por Mazzamuto *et al*. (2019) en una investigación de similares características, con enfoque en el puercoespín crestado (*Hystrix cristata*, Hystricidae, Rodentia). Para poder explorar a mayor profundidad los factores que pueden influenciar la probabilidad que la especie esté presente y sea detectada, se procedió a correr los modelos que incluían las variables previamente mencionadas.

Al incorporar dichas variables en los modelos explorados, se pudo observar un ajuste en la probabilidad de ocupación de *A. boliviensis*, mostrando un potencial aumento de un 4 % con respecto a la ocupación ingenua para ambas épocas (Tabla 1). Dentro de las variables exploradas para la época seca, se pudo observar que el modelo de la cámara utilizada es la variable de muestreo que influenció la probabilidad de detección de la especie (24 % época seca y 36 % época húmeda), siendo Bushnell TrophyCam la cámara con mejor rendimiento. En cuanto a las variables del sitio, el hábitat rocoso explica mejor la probabilidad de presencia de la especie. Por tanto, el mejor modelo correspondiente a la época seca, es aquel que ajusta la probabilidad de presencia de la especie de acuerdo al hábitat rocoso y al efecto del modelo de la cámara para la detección de la misma.

Tabla 1. Lista de los mejores modelos para nuestro análisis exploratorio, donde: K = número de parámetros. AIC = valor del Criterio de Akaike, ΔAIC = diferencia del valor AIC del modelo con respecto al modelo con el menor valor para AIC, w_i = peso del modelo, Ψ = probabilidad de ocupación, ρ = probabilidad de detección, SE = error estándar.

	Modelo	K	AIC	ΔAIC	w_i	Ψ	SE
Época Seca	Ψ(hábitat rocoso)ρ(.)	3	220.70	0.00	0.5500	0.3376	0.1022
# detecciones = 33	Ψ(.)ρ(modelo de la cámara)	3	221.54	0.84	0.3614	0.3848	0.0874
Naïve occupancy = 0.3023	Ψ(.)ρ(.)	2	224.35	3.65	0.0887	0.3300	0.0799
Época Húmeda	Ψ(sustrato rocoso)ρ(.)	3	403.16	0.00	0.8367	0.3404	0.0787
# detecciones = 95	Ψ(presencia predador)ρ(.)	3	406.47	3.31	0.1599	0.3400	0.0814
Naïve occupancy = 0.3396	Ψ(.)ρ(.)	2	414.13	10.97	0.0035	0.3402	0.0652

Para la época húmeda, el sustrato rocoso y la presencia de su depredador fueron las variables con mayor efecto. En cuanto al hábitat y el sustrato, de acuerdo a lo esperado, la presencia de *A. boliviensis* parece estar positivamente relacionada a ambientes que presenten ya sea un sustrato y/o ambiente rocoso. Finalmente, la correlación entre la presencia de la especie en estudio y su predador principal podría dar pautas sobre la probabilidad de encontrar a este elusivo roedor en futuros diseños enfocados en el estudio de *A. boliviensis*.

Discusión

Para la región de Tarija, localizada en el sur de Bolivia, los presentes registros de una especie de rata chinchilla representarían los primeros y los más australes del país. En el área de Aiquile las fotografías de *A. boliviensis* representarían los primeros reportes para esta región en el departamento de Cochabamba. Si bien la utilización del foto-trampeo no es la técnica de preferencia para el estudio de animales de pequeño tamaño, este trabajo demostró su utilidad para la obtención de datos sobre roedores de difícil captura, como *A. boliviensis*. Los resultados obtenidos por De Bondi *et al.* (2010) también comprobaron la potencialidad de este método de muestreo, especialmente en la tasa de capturas y su utilidad en registrar especies elusivas. Además, es un método que permite realizar evaluaciones rápidas, determinando los atributos a los que una especie o un conjunto de ellas puedan deber su presencia (MacKenzie *et al.* 2006; Kalies *et al.* 2012).

Los registros de *A. boliviensis* obtenidos en este estudio en la región central de los Andes bolivianos refuerzan el conocimiento sobre la relación de la especie hacia ambientes con características rocosas, coincidiendo con las observaciones de Tarifa *et al.* (2009).

Respecto a los otros factores que difieren entre épocas debemos tratar por separado los aspectos relacionados al conocimiento de la especie y los factores metodológicos del muestreo. Primeramente, al ser la especie elusiva, principalmente con actividad nocturna y de porte pequeño presenta una baja detectabilidad que, sumada a la baja cantidad de registros obtenidos para cada época, no permiten construir modelos más complejos y por ende indagar en las variables que determinan la presencia de la especie en los bosques secos de la ecorregión Boliviana-Tucumana. Por tanto, cuando se trataron de construir modelos con más de una variable, estos no pudieron converger. Thomas *et al.* (2020) menciona la baja detectabilidad como limitante para el análisis y para la conducción a estimaciones sesgadas de las preferencias del hábitat (Ferreguetti *et al.* 2018b; Gorosito *et al.* 2018) sumado a una diferencia marcada entre épocas en el lugar de estudio (Chutipong *et al.* 2017). Por consiguiente, se considera necesario colectar datos futuros, aplicando un diseño específico para la especie, para explorar si se mejora la probabilidad de detección y genere mayor cantidad de datos.

Otro factor relacionado a la probabilidad de la presencia de *A. boliviensis*, son los registros del gato mediano *Leopardus geoffroyi* en la época húmeda. Este dato muestra la estrecha relación presa-predador, considerando que un roedor de tamaño considerable como *A. boliviensis* llegaría a ser la presa ideal en ambientes como los bosques Boliviano-Tucumanos o hábitats de la ladera oriental de los Andes centrales donde ambas especies confluyen (Anderson 1997; Noss *et al.* 2010). Probablemente esta variable mostró tener efecto solo en la época húmeda debido a la distancia a cuerpos de agua es una variable determinante para la presencia de felinos (Wilting *et al.* 2010). Ya que la marcada estacionalidad de estos bosques (Josse *et al.* 2009) presiona a este felino a quedarse en áreas más cercanas aguas permanentes durante la época seca y, por tanto, reducir el número de encuentros con *A. boliviensis*. Trabajos de trampas cámara dirigidos a esta interacción felino-roedor confirmarían aspectos ecológicas de estas especies (Suselbeek *et al.* 2014; Chutipong *et al.* 2017). Además, este resultado tiene un valor importante en futuros estudios de *A. boliviensis*, puesto que los indicios de *L. geoffroyi* podrían usarse como elementos para considerar sitios de muestreo y, posiblemente, aumentar la tasa de captura.

Analizando los aspectos metodológicos del muestreo se observa que, para la época seca, el factor tipo de cámara, está relacionado con la probabilidad de detectar la presencia de *A. boliviensis*, esto se debe a la sensibilidad que cada modelo de cámara presenta. De acuerdo a los resultados obtenidos se puede concluir que Bushnell TrophyCam tiene mayor éxito al registrar animales de menor envergadura. Muchos estudios resaltan que se deben considerar las características de diferentes modelos y marcas de cámaras, previo al diseño del muestreo (Rovero *et al.* 2013;

Meek *et al.* 2014; McCleery *et al.* 2014; Thomas *et al.* 2020) Hay que recalcar que, si bien los datos usados han servido para mostrar la probabilidad de ocurrencia de este roedor, el diseño y disposición de las trampas cámara fueron diseñados para mamíferos grandes, objetivo de estudio del PCCA. Además, es importante considerar que las especies de menor tamaño presentan una menor tasa de captura (Tobler *et al.* 2008); sin embargo, y a pesar de no haber cumplido un diseño específico para la especie en estudio, se lograron obtener más de 100 registros de *A. boliviensis*, un número virtualmente imposible de obtener utilizando métodos de captura tradicionales.

Con el presente trabajo se demuestra que el uso de trampas cámara es una opción viable en el trabajo con mamíferos de porte mediano a pequeño. Los roedores, por su gran diversidad taxonómica y abundancia, tienen grupos únicos que atraviesan amenazas con altas tasas de extinción. Éstos aún tienen la necesidad de mayor conocimiento acerca de su rol en el ecosistema, valor como especie o importancia en comunidades locales. Las limitaciones en el muestreo con trampas de captura viva pueden ser complementadas con el uso de trampas cámara, optimizando esfuerzos de muestreo y maximizando el conocimiento científico (De Bondi *et al.* 2010; Edwards 2018). Los resultados obtenidos con este método pueden ayudar a definir el estado poblacional de pequeños mamíferos, también puede significar un método efectivo para monitorear la eficacia de las medidas de conservación aplicadas a estas especies. Por ello, para aumentar el conocimiento de la historia natural de *Abrocoma boliviensis*, especie elusiva, rara y en peligro crítico de extinción, se considera que futuros estudios deberían complementar métodos tradicionales de muestreo con foto-trampeo, para determinar probabilidad de presencia, uso de hábitat y patrones de distribución, y así desarrollar acciones de conservación con base científica.

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Reproductive adaptations to high densities in social mammals

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An overview of population density control in social mammals sets the framework for examining reproductive responses to increasing population densities. We begin by honoring John B. Calhoun who played a major role, starting about 70 years ago, in correcting the conventional wisdom of the time that population control was all about adjusting mortality rates. Reproduction was considered a constant, and emigration was viewed as a component of mortality. His research was mostly on domestic and feral populations of *Rattus norvegicus* and *Mus musculus* for which he built complex arenas that could house thousands of inhabitants. In addition, he constructed elaborate living quarters in the alleyways of Baltimore. For the captive populations, he would individually mark all the inhabitants so that he could identify them and observe their behavior. Eight examples of his research publications are described. He was able to document a list of reproduction related behaviors that are the main focus of this essay, and clearly demolish the simplistic notion that reproduction is a constant. A summary of some of the major issues that encompasses the science of population growth and regulation is provided. There follows a series of 19 examples of non-Calhoun publications that cover many more species of social mammals, including humans. A comprehensive list of the many negative adaptations involving reproductive processes are documented for the 27 publications reviewed confirming that in many species reproductive constraints are non-trivial. There follows a brief discussion that attempts to create a cohesive whole for this intellectual adventure.

En este articulo, se presenta una reseña histórica sobre estudios de control de densidades poblacionales en mamíferos sociales, lo que establece un marco de referencia para examinar las respuestas reproductivas al incremento en densidades poblacionales. Comenzamos honrando a John B. Calhoun, quien, comenzando unos 70 años atrás, y jugó un papel importante pues corrigió las creencias convencionales de la época de que el control de la población se basaba solamente en el ajuste de las tasas de mortandad. La reproducción se consideraba una constante, y la emigración se consideraba un componente de la mortalidad. Sus investigaciones se centraron principalmente en poblaciones domésticas y silvestres de *Rattus norvegicus* y *Mus musculus*, para las que construyó arenas complejas que podían albergar hasta miles de individuos; además, construyó elaboradas viviendas en los callejones de Baltimore. Para las poblaciones cautivas, marcaba individualmente a todos los habitantes para poder identificarlos y observar su comportamiento. Se describen ocho ejemplos de sus publicaciones de investigación. Calhoun pudo documentar una lista de comportamientos relacionados con la reproducción que son el foco principal de este ensayo y claramente desmantelan la simplista noción de que la reproducción es una constante. Se proporciona un resumen de algunos de los principales temas que abarca la ciencia del crecimiento y la regulación de la población. A continuación, se presenta una selección de 19 otras publicaciones que cubren muchas más especies de mamíferos sociales, incluyendo los humanos. En las 27 publicaciones examinadas se documenta una lista completa de las numerosas adaptaciones negativas que entrañan los procesos de reproducción, lo que confirma que, en muchas especies, las limitaciones en materia de reproducción no son triviales. Por último, se presenta una breve discusión que intenta crear un todo cohesivo para esta aventura intelectual.

Keywords: cannibalism; density controls; dispersal; ecology; homosexuality; J. B. Calhoun; reproduction constraints; social behavior; social groups; stress.

Introduction

Ecologists understand that as populations grow, negative forces gradually accumulate that eventually stop growth or even precipitate population crashes. There are three possible forces that either separately or in various combinations lead to growth slowing and eventually cessation. These are increasing mortality, decreasing reproduction, and emigration rates exceeding immigration (Cole 1948; Lidicker 1985; Park 1946). In a global perspective, only the first two of these are relevant. This essay explores the various ways that reproduction in highly social mammals respond to increasing densities. For a conceptual framework of population regulation in mammals developed in a historical narrative see Lidicker (1983, 1994).

Mammals like all other organisms require multiple resources for their success. For mammals these include food, adequate shelter, protection from predators and parasites, a physical and biotic environment or habitat appropriate to their needs, and opportunities to reproduce. If a species reproduces sexually, like mammals, a further requirement is a suitable social environment that can then supply the necessary sex partners. In some cases, success requires more than one habitat. A species of bat for example may need a cave in the winter and a forest at other times of the year, or a pinniped will rotate on an annual cycle between a safe haul out site and the open ocean. A rodent may use an agricultural field in the summer but require a more sheltered burrow at other times.

Another ecological principle that needs including in this brief outline of demographic processes is the so-called Allee effect (Lidicker 2010), also termed anti-regulation. It turns out that there are sometimes forces that operate in directions opposite the regulating ones outlined above. For example, Allee effects may promote growing populations to increase faster as numbers increase rather than more slowly. Eventually regulating influences will overcome the anti-regulating ones and growth does stop. Also, the Allee effect can operate at low densities. In this situation, growth promoting forces ordinarily increase as numbers decrease, but if anti-regulating forces are present a population will instead continue to decline, and then if it drops below a certain threshold density, it will continue to decline to extinction.

Given this brief outline of demographic processes, I now focus on possible reproductive declines at high densities, especially in mammals. Of course, mammals are subject to the full suite of negative forces outlined above. However, there is increasing evidence that mammals have mechanisms for reducing reproductive success at high densities that are not directly caused by the usual resource and habitat limitations. So far, the evidence for this comes from highly social species, and therefore we can surmise that it may be somehow related to overly intense or overly stressful social interactions at high densities.

In the early days of modern population ecology, that is going back about seven decades, it was widely proclaimed that reproductive activities did not decline with increasing densities, but instead population control was largely an effect of mortality increases. Even dispersal from high density areas was thought to not be very important because dispersers were supposedly quick to be converted into mortality statistics (Lidicker 1978). It was in this intellectual environment that John Calhoun began his experimental work on mammal population dynamics starting in about 1949 and extending to at least 1963. Some research was done on wild populations of rodents (Calhoun 1962a, 1962b), but mostly he focused on captive colonies living in large and complex enclosures that, sometimes housed individuals numbering in the thousands. In this way he could observe and analyze their social behavior in detail, and match it with reproductive activities, lifespan, causes of mortality, etc. The species he used were *Rattus norvegicus*, both wild and domesticated, and various strains *of Mus musculus*.

A John B. Calhoun Sampler. The first part of this document is written as a tribute to Calhoun in appreciation for his pioneering contributions to population ecology and social behavior of mammals. His contributions have been truly monumental. Here is a chronologically arranged sample of Calhoun's publications (*n* = 9) with comments explaining their relevance to our current topic (see publication index for full citations).

1. Calhoun (1949). Observations of five rat colonies in very large pens constructed in Baltimore alleys and streets. The rats used in this experiment came from a small island and so were judged to be relatively inbred. The rate of reproduction was negatively related to the density of the population. New born young from mothers with poor nutrition failed to survive. The extent to which fetal nutrition was sub-maximal slowed population growth. Lactating females were particularly aggressive toward low ranking females. Slow growing females received 10 times more wounds than those fast growing. Larger and more dominate females raised 10 litters from 12 pregnancies while subordinate females weaned a maximum of one litter. The conclusion is that social conditioning may be a potent factor in population control among mammals.

2. Calhoun (1950). This paper reports results using the same enclosures as the previous paper. Five pairs of rats were used to initiate the colony. Rats raised in a suboptimal part of the enclosure weighed less, were more frequently wounded, conceived less often, and only rarely raised a litter successfully compared to other rats. That is, the rats living in the less favorable areas were "socially sterilized." Some of these females had young, but they survived only a few days. This example illustrates the potential importance of micro-habitat quality in influencing reproductive success.

3. Calhoun (1952). Social stability through formation of social groups led to successful reproduction and decreased mortality, but eventually population growth restricted use of all the available space. This, along with groups lacking well integrated dominance hierarchies caused social instability that reduced the frequency of conceptions. Moreover, very few of the young born lived to weaning, and those few that did survive had only a slim chance of breeding. The importance of the Allee Effect at both high and low densities was also reported.

4. Calhoun (1956). Mouse strains differed in their susceptibility to social stresses. Adult males were the major stressors of adult females, and if new mothers were socially stressed by males, they ate their young shortly after birth. Stress also occurs if the social environment becomes more complex, and this also can disrupt maternal care behavior. Adjustment to more complex social and/or physical environments as well as higher densities is sufficient stress to disrupt maternal behavior. This results in both failures to conceive and destruction of litters. In one experiment, a new colony consisting of 14 adults and 15-day-old young were all dead within 75 days apparently a consequence of fighting. Lower densities were achieved by dispersers forming very small colonies presumably in order to establish persistent and positive social relationships quickly, and this generated an overall lower density (number of individuals per square yard).

5. Calhoun (1961). One colony of domestic rats grew for four months to peak density, producing three generations of young organized into complex social structures. Relevant features were persistent within litter social associations, harem formation, homosexuality, and stable social groups.

6. Calhoun (1962a). This research involved laboratory rats and featured acutely abnormal behavior leading to extinction. Initially there were 80 individuals in 4 pens. All the rats were in good health and were at the prime of life age. They produced fewer litters than expected;

none of the offspring lived to maturity; males were more homosexual or "pansexual" (made sexual advances to males,females not in estrous and juveniles); some mles were indifferent to all other individuals, even females in estrous. These homosexual males were ignored by other rats and seemed perfectly healthy. There were also some males labeled "probers" These males were hyperactive, hypersexual, and homosexual, and some became cannibalistic; only half of newborns survived. The colony continued to deteirorate.

7. Calhoun (1962a). The colony in this study took four months to reach peak density; it featured territoriality, harem formation, social stability, and homosexuality. Reproduction was inhibited in two ways by social stresses: 1) a reduced ability to rear the young such that no young survived to maturity even though the number of conceptions (placental scars) was not reduced, and 2) a reduction in the ability of fertilized eggs to develop following implantation. These two phenomena are believed to be the most important ones through which population growth was inhibited in the presence of abundant food and an sample space for the elaboration of new burrows.

8. Calhoun (1962b). When a population of laboratory rats is allowed to increase in a confined space, the rats develop acutely abnormal patterns of behavior that can even lead to the extinction of the population. Many of the females were unable to carry pregnancy to full term or to survive the birth of their litter. If they did successfully deliver their litter they failed in their maternal duties, and the litter did not survive. Males mostly developed behavioral disturbances ranging from sexual deviations to cannibalism, and from frenetic over-activity to pathological withdrawal from social interactions. The sex ratios of social groups became aberrant, and infant mortality reached 96 % in some social groups. Of special interest, many adult males assumed various pathological behaviors. Some became aggressive to all other individuals regardless of sex or age. Many became homosexual, and some were “pansexual” as they did not discriminate among sexes or ages, but sexually assaulted one and all. Others moved through the communities ignoring all other rats, even females in estrous, and if attacked they did not attempt to retaliate. Some adult males adopted a new type of behavior that the author named “probers”. They were hyperactive, hypersexual, homosexual, and for some cannibalistic. When they did encounter an estrous female, they ignored all the usual courtship procedures that are typically performed. Obviously social groups that developed in this way did not have a happy future.

9. Calhoun (1963). The author postulated that the natural or basic group size for social mammals is 12. If population growth causes this optimal group size to be exceeded, frustration increased in concert with increasing population density, and this in turn lead to increasing presence of males that deviate behaviorally from the usual norm, homosexuality being a common variant. He also claimed that Vitamin A reduced social group stress. Significantly, the author also suggested that human social behavior is consistent with the basic structure that is found in other social mammals investigated, including the occurrence of aberrant reproductive behaviors such as homosexuality.

Other relevant contributions. Here are brief descriptions of 19 publications, not including any of those authored by John Calhoun. Mostly they are about small mammal populations, both in confinement and in free-ranging that illustrate the diversity of ways that reproduction influences population regulation. In order to honor the historical framework of this document, the 19 publications are arranged in chronological order of their publication date, starting with the oldest one.

1) Anderson (1961), species featured: House mouse *(Mus musculus*). The concentration is on house mice living in the more traditional agricultural environments in which favorable sites with abundant resources are scattered widely. If immigration pressure to a favorable site is intense and resources are compromised, the social stability of the social group will be damaged, precipitating gonadal inhibition, cannibalism of young, and nest destruction.

2) Barbehenn (1961), species featured: laboratory rat (*Rattus norvegicus*) explores the relationship between the tendencies for newly weaned laboratory rats to explore their environment depending on the size of the litter in which they were raised for 30 days after birth. Members of litters of 12 began to explore within one or two days after the chambers were opened. Those from litters of 3 were not all exploring until 65 days of freedom. Those from litters of 6 were intermediate in their enthusiasm for exploration. The large litter cohorts were also the most aggressive of the three categories in feeding. There can be no doubt that the weanlings from litters of 12 would have the best chance of initiating their own reproductive fitness promptly. After about 90 days the exploratory behavior of all three categories of litter size had equilibrated**.**

3) Lidicker (1965), describes a comparative study in population regulation using four species of rodents that were introduced separately into large complex chambers with multiple levels, complex passageways, nest chambers, feeding areas, etc. The species tested were*:* *Mus musculus*, *Peromyscus maniculatus, P. truei*, and *Oryzomys palustris*. Two adults were introduced into each of the complex chambers supplied with excess food and water. The experiments lasted from one year to 2.5 years. Six populations were observed. The two *P. maniculatus* and one *Mus* populations exhibited density plateaus due to seasonal cessation of reproduction combined with much nestling mortality. Also, sex ratios became biased in favor of males, and these males had

extensive wounding and other signs of stress. The *Oryzomys* and *P. truei* populations experienced much infant mortality and a small but persistent amount of adult mortality. These two species do not ordinarily experience high densities, and so it seems that they have not evolved mechanisms to deal with such densities and therefore resort to killing when densities are high.

4) Lidicker (1976), concerns a study of house *mice* (*Mus musculus*) living in two large and complex enclosures. The colonies were established by introducing 15 pairs of adults to each enclosure. Both grew rapidly to about 2,000 individuals in one and somewhat less in the other. The mice became arranged into eight social groups. In both populations successful dispersal among groups was very rare. In fact, the dispersing weaned young almost invariably returned to their home group. Three attempts were made to introduce additional mice. This was only successful when the newcomers were able to establish a new group in disputed areas between established groups. Continued growth of existing groups was prevented by reproductive inhibition and high neonatal mortality. There was massive inhibition of sexual maturation in young mice as well as complete regression of reproductive tracts in most adults. Such mice tended to get fat and there was a negative relationship between obesity scores and the size of the seminal vesicles. Moreover, there was widespread failure of adults to become reproductively active and a widespread loss of neonates during the first three days after birth. Older mice that had matured sexually tended to regress from reproductive competence in both sexes.

5) Lidicker (1979). Subject species: California vole (*Microtus californicus*). These voles were introduced into two large enclosures with natural grassland vegetation cover. Population founders were two pairs of adult voles in each enclosure. Initial fighting reduced the founders to one pair in one case and one male and two females in the other. Adequate food and water were supplied throughout. The populations grew rapidly with all three of the surviving founders breeding successfully. However, neonatal mortality was high although litter size was unaffected. A large percentage of the adults of both sexes were initially involved in the population growth. However, by half way through the about one-year experiment, a high percentage of the adults failed to mature sexually, and the three founding voles abruptly disappeared.

6) Lidicker (1980). Subject species: California vole (*M. californicus*) summarizes information from a number of field and captive studies on the social biology of the California vole. Increasingly high densities suffer increasing proportions of sexually inactive adults. The inhibitory effects are stronger in males than in females. In one high density year only 20 percent of the males were reproductively active. Over a three-year study males weighings less than 35 grams were uniformly inactive sexually. Those more than 45 g were all reproductively active. This effect occurred in both enclosures and natural habitats. In a year of peak densities, only 20 % of males were reproductively competent. This syndrome also occurs in *Microtus agrestis*.

7) Cockburn and Lidicker (1983). Subject species: California vole (*M. californicus*). This research was done in natural grasslands. The largest males in four monitored populations tended to move to the lowest quality grids which had few adult females, and therefore contributed little to reproduction in the population collectively.

8) Lidicker and Ostfeld (1991). Subject species: (*M. californicus*). This report is on an unusual behaviorally caused reduction in reproductive output in the California vole, and by extrapolation likely also occurring in other species of *Microtus* that exhibit multiannual cycles of abundance. As populations approach their peak densities, it was observed that the largest and presumably the oldest males accumulate in the poorest habitat patches. Adult females are rarely found in these places and hence a major depression in potential reproductive output occurs. One could speculate that selection is favoring the fitness of previous offspring of these large males as population densities are approaching a crash in numbers. Or perhaps these large males are merely avoiding aggression from younger adult males.

9) Lidicker (1994), provides an overview of population dynamics with an emphasis on mammals, in an historical perspective.

10) Lidicker and Batzli (1999). Subject species: Singing vole (*M. miurus*) occurs in the northwestern most part of North America where it lives in well drained tundra and subalpine zones. Their density fluctuates strongly with declines associated with poor reproduction. A few pregnancies can occur at any time of the year but they are rare at any time, presumably as a result of chronically scarce food resources.

11) Lidicker *et al.* (2000). Subject species: Snowshoe hare (*Lepus americanus*). Observations of genetic changes within a single 11-year population cycle of the snowshoe hare suggests the possibility that such genetic shifts could be an additional influence on modifying reproductively relevant behaviors.

12) Lidicker (2009), provides an overview of population dynamics as of a decade ago, and includes a look into the past, and makes projections for the future. Most importantly it reveals how the trend over the past seven decades has seen a gradually increasing level of complexity in the context of ecological research (up to the ecoscape level). In particular, the trend has revealed increasing examples of reproductive responses to high population densities.

13) Schoepf and Schradin (2012). Research subject is the African striped mouse (*Rhabdomys pumilio*). This species is socially flexible and can live successfully in

groups or solitarily. This research attempts to understand how individuals cope with and profit by this flexibility. There are seasonal changes, as well as unanticipated environmental fluctuations, and possible genetic changes. There is some evidence that individuals begin to develop behaviors appropriate to anticipated dispersal targets before they actually move. For example, mice anticipating a move become more active before actually dispersing. Aggressive behavior is correlated positively with body weight.

14) Schradin and Lindholm (2012). Subject: African striped mouse (*R. pumilio*). Flexible social behavior allows for adaptations to changing conditions, and provides especially for conditions favorable for reproduction. Behavioral changes are driven by sex hormones. Most dispersers are males. High population density favors group living and philopatry.

15) Raynaud and Schradin (2013). Subject: African striped mouse. Breeding is stimulated by high blood levels of prolactin. This is normally controlled by photoperiod. However, unusually favorable food conditions or unseasonable rainfall can also cause an increase in prolactin and can trigger breeding behavior.

16) Manjerowic and Waterman (2015). Subject: Cape ground squirrel (*Xerus inauris*). Sixty five percent of males that attend to a female in estrous successfully copulate, and this is the same for resident and dispersing males. However, 70 % of completed copulations do not result in any offspring. On the population level, only 28.4 % of males succeed in fathering offspring. Normal litter size is one, and in the rare cases of two embryos, each fetus has a different father. Typically, these squirrels live through two breeding seasons.

17) Nater *et al.* (2018). Subject: African striped mouse. Modeling study focused on effects of environmental temperatures, food supply, and density changes on reproduction. Strong density feedbacks allowed reproduction to stabilize densities and recover from detrimental crashes. There is no mention of how density translates functionally into variations in reproduction, but food supply is the primary driver. This study is a classic example of density-dependent control of demographics.

18) Wadman (2018). Subject species: (*Homo sapiens*) describes a paper published in Plos One by Lisa Littman that describes a sudden increase in gender dysphoria among human teens and young adults. It is of course controversial and it has attracted much critical commentary. Critics have claimed that the paper was not good science and was politically biased. One writer even made the inexplicable comment that the article was "anti-gay." Littman's paper includes a graph showing an exponential growth in transgender identities of both sexes from 2009 to 2016. Wadman concludes that Littman's paper points to a clearly real phenomenon. My suggestion on this controversial paper is that it is arguably "pro-gay" since it adds understanding to the current reality.

19) Van Cann *et al.* (2019). Subject: Bank voles (*Myodes glariolus*). Early life of fathers has major fitness effects on offspring. These influences lead to a mechanism for fathers to transmit environmental information to their offspring. That then promotes adaptation to current density conditions. Experiments were carried out in outdoor experimental cage systems that were semi-natural. Reference is made to earlier studies on maternal social stresses leading to reduced body mass of offspring.

Discussion

In this treatise I have tried to amalgamate basic population ecology with a comprehensive look at the role of reproduction in contributing to regulation of population numbers with an emphasis on social mammals. The importance of mortality in this regulation process is widely acknowledged, and dispersal is increasingly investigated for its role in spatially organizing and thereby stabilizing ecological communities, and therefore in stopping population growth. The literature seemed to point to highly social species as likely to have the most complex and interesting possibilities for finding controls on reproductive functions. Moreover, this focus also includes our own species which with our runaway population growth and the myriad of related problems definitely needs to be included. I think this remains a fascinating and potentially rewarding frontier for research, and I hope that this paper will stimulate research on the role of social behavior in mammals especially with a focus on its demographic and conservation impacts. Rewarding research opportunities abound.

While it is true that emigration from high density enclaves with or without increasing mortality rates can in principle stop population growth and even initiate population declines it is also true that reductions in reproductive outputs can also accomplish this. And, of course all combinations of the three relevant demographic processes can and do occur. Moreover, all of these possibilities can be found in captive populations as well as those free ranging.

Selected 16 examples of social behavior/density coactions. Our goal is to document and understand the nature of both positive and negative behavioral synergisms. With goal in mind, here is a list of 16 reproductive processes found in this short literature survey of 27 publications that have been observed to have negative effects on population growth. They are described in more detail both in the section of papers by John Calhoun and in the section on "other relevant contributions":

a. Failure of pregnancy to go full term; neonates all dead by three days post-partum;

b. Spatial segregation of adults with largest males accumulating in the poorest habitat patches, adult females mostly absent; failure of young to reach sexual maturity;

c. Lactating females aggressive toward low-ranking females who raised only one litter compared to 10 by dominant females over the same time period;
d. High densities cause de-stabilization of social groups that then have few conceptions, and those few young that do survive have only a slim chance of breeding;
e. Harem formation reduces female mating, and homosexuality reduces male breeding;
f. Social instability and accompanying stress lead to no young surviving to sexual maturity, and pregnancies not reaching full term;
g. Some females are unable to survive parturition; successful parturition may be followed by death of the litter; males can become cannibalistic;
h. Social instability leads to no young surviving to maturity, females may be unable to survive parturition or maybe followed by successful parturition may be followed subsequently by death of the litter;
i. Massive inhibition of sexual maturation in young mice and complete regression of reproductive tracts;
j. A negative relation between obesity scores and the size of seminal vesicles;
k. Older mice that have matured sexually tend to regress from reproductive competence in both sexes;
l. Intense social pressure causes social groups to become unstable leading to gonadal inhibition, cannibalism of young, and nest, destruction;
m. Sex ratios become biased in favor of males leading to extensive wounding and other signs of stress;
n. Species that normally do not experience high densities resort to killing when densities are high;
o. As the population increases, the fraction of the adult population that is not-reproductive increases, males are more subject to reproductive loss than females;
p. The timing of exploration by neonates is positively correlated with litter size in litters varying from three to twelve and those from large litters are the most successful in integrating into the social environment and beginning their reproductively active life.

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Altitudinal variation of species composition of small non-flying mammals in the Yungas region of Bolivia

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The Cotapata National Park and Natural Area for Integrated Management (PN-ANMI) is located on the eastern escarpments of the Eastern Cordillera in Bolivia. It has an altitudinal range between 1,100 to 5,600 masl, with five altitudinally delimited ecological zones. There is great variability of environments, which generates great animal species diversity, varying according to elevation, and in association with changes in climatic and ecological conditions. The aim of this study was to determine the pattern of richness and composition of small non-flying mammals along an altitudinal gradient in the PN-ANMI Cotapata and to evaluate responses of these species to the gradient. We worked at three different elevations: Yungas Forest (1,400 masl), Cloud Forest (2,100 masl) and Yungas Paramo (3,500 masl). Six temporary replicas were conducted. For each sampling period we run three 250 m linear transects were placed, separated by 50 m attitudinally. Each transect contained 25 sampling stations, with two snap traps. With the exception of Yungas Paramo (due to the rocky ground), we also run transects of pitfall barrier traps (five buckets, every 5 m). We captured 460 specimens corresponding to 20 species of rodents and two of marsupials. Although, species richness (S) and diversity ($Cinv$) were higher in Cloud Forest (intermediate elevation; $S = 11$, $Cinv = 4.30$), followed by Yungas Forest ($S = 9$, $Cinv = 3.47$), and lower in Yungas Paramo (higher elevation; $S = 8$, $Cinv = 2.12$), only the diversity was significantly different ($H = 7.0$, $n = 17$, $P = 0.03$). Species composition varied between places, showing the greatest turnover between Cloud Forest and Yungas Paramo, with a similarity of only 2 %. Yungas Paramo had the highest number of exclusive species (seven of the eight registered). The diversity was higher at medium altitude, giving a positive monoclinal hump-shaped pattern. This variation, responds to climatic influences associated with changes in vegetation, where Cloud Forest provides a greater diversity of ecological niches. The lower diversity in Yungas Paramo, and the almost total species turnover responds to inhospitable and stress conditions and to the physiological adaptations of these species to these elevations.

El Parque Nacional y Área Natural de Manejo Integrado Cotapata (PN-ANMI) se encuentra en la región cordillerana oriental de Bolivia. Presenta intervalo altitudinal desde 1,100 hasta 5,600 msnm, albergando cinco pisos ecológicos limitados altitudinalmente. Esto genera una gran variabilidad de ambientes, no solo entre pisos ecológicos, sino al interior de los mismos. Esta variabilidad genera una gran diversidad de especies animales que variaría según el incremento en la elevación y; por ende, al cambio en las condiciones climáticas y ecológicas asociadas. Así, este estudio busca determinar el patrón de la riqueza y composición de pequeños mamíferos no voladores a lo largo de un gradiente altitudinal en el PN-AMNI Cotapata y evaluar las respuestas de estas especies a dicho gradiente. Se trabajó en tres diferentes elevaciones que coinciden con los tres pisos ecológicos inferiores: Bosque Yungueño (1,400 msnm), Bosque Nublado (2,100 msnm) y Páramo Yungueño (3,500 msnm). Se realizaron seis réplicas temporales (épocas seca y húmeda y sus transiciones). En cada muestreo se colocaron tres transectos lineales de 250 m, separados altitudinalmente por al menos 50 m. Cada transecto contenía 25 estaciones de muestreo, con dos trampas golpe. En el Bosque de Yungas y Bosque Nublado se colocaron tres y dos transectos de trampas de barrera pitfall (respectivamente) con cinco baldes cada una, separados por cinco metros; en el Páramo Yungueño no se los pudo instalar debido al suelo rocoso. Se capturaron 460 especímenes correspondientes a 20 especies de roedores y dos de marsupiales. Si bien riqueza (S) y diversidad (Inverso de Simpson, $Cinv$) de especies fueron mayores en el Bosque Nublado (elevación intermedia; $S = 11$, $Cinv = 4.30$); seguido por el Bosque Yungueño ($S = 9$, $Cinv = 3.47$) y menor en el Páramo Yungueño (mayor elevación; $S = 8$, $Cinv = 2.12$); solo la diversidad fue significativamente diferente ($H = 7.0$, $n = 17$, $P = 0{,}03$). La composición de las especies varió entre los pisos, observándose una mayor diversidad beta entre Bosque Nublado y Páramo Yungueño, con una similitud de solo del 2 %. Páramo Yungueño presentó el mayor número de especies exclusivas (siete de las ocho registradas). La diversidad fue mayor a altitud media (Bosque Nublado), dando un patrón monoclinal positivo con forma de joroba. Esta variación, y en especial el recambio de especies observado, particularmente entre los dos pisos ecológicos superiores, respondería a las influencias climáticas asociadas con cambios en la vegetación, donde Bosque Nublado proporcionaría una mayor diversidad de nichos. La menor diversidad en el Páramo Yungueño, y el recambio casi total de sus especies respondería a las condiciones inhóspitas y de estrés climático, donde especies con adaptaciones fisiológicas a dichas condiciones tendrían una ventaja competitiva.

Keywords: altitudinal gradient; Cotapata National Park; distribution; rodents; eastern mountain range; non-volant small mammals; replacement.

Introduction

Environmental gradients, such as latitude, altitude, sea depth, are responsible for the perceived patterns of abundance, distribution, and diversity of organisms on earth (Brown 2001). The decline in species richness from the equator to the poles is one of the most universal biogeographic patterns, demonstrated in a variety of taxa in aquatic and terrestrial ecosystems (Rahbek 1995). A similar pattern has been suggested to occur in altitudinal gradients, with richness decreasing monotonically as elevation increases (Stevens 1992; Brown 2001), as observed for neotropical birds (Terborgh 1977; Brown 1988; Herzog *et al.* 2005) and amphibians (Navas 2006). Altitudinal gradients are particularly important because they are often associated with abiotic gradients (climate, humidity and exposure), which in turn may generate structural complexity and habitat heterogeneity (Körner 2007; Heaney 2001; Lomolino 2001). Further, increased structural complexity and habitat heterogeneity provide resources (*e. g.*, food and shelter), which generate intra- and interspecific competition (MacArthur and MacArthur 1961). All these factors have an impact on the richness, diversity and species assemblage of a given location (Luévano *et al.* 2008; Cruz *et al.* 2010) and, therefore, on alpha or beta biodiversity (Lomolino 2001; Sanders and Rahbek 2012).

Changes in species richness are not necessarily monotonic or clinal (increasing or decreasing; Rahbek 1995; Sanders and Rahbek 2012), and may be unimodal (hump-shaped pattern) positive or negative (Rosenzweig 1992). Several studies, conducted on small non-flying mammals in various regions of the world found unimodal (hump-shaped) patterns with peaks of richness at medium elevation (Patterson *et al.* 1998; Kelt 1999; Heaney 2001; Md Nor 2001; Rickart 2001; Sánchez-Cordero 2001; McCain 2003, 2004). This pattern corresponds to the predictions proposed by the null model hypothesis of the mid-elevation domain (Colwell and Hurtt 1994; Colwell and Lees 2000). McCain (2005, 2007) analyzed the relationship between elevation and species richness of small mammals and found a clear pattern of medium elevation peaks in species richness (humped pattern), although few data completely matched the predictions of the null model. These and subsequent studies ruled out the null model as responsible for this pattern (Currie and Kerr 2008; Bateman *et al.* 2010; Andrade and Monjeau 2014), where ecological factors such as climate (temperature, precipitation), productivity, and habitat heterogeneity provide environmental explanations for the richness gradients.

In South America, Mena *et al.* (2011) reviewed the work done in the tropical Andes and the relationship of elevation with the diversity of small non-flying mammals (mainly in Peru and Colombia). There is no consensus on a general pattern that describes how small mammal fauna diversity changes with elevation in the Neotropics (Patterson *et al.* 1989, 1998; Villalpando 2004; Vivar 2006; Swenson *et al.* 2012; Andrade and Monjeau 2014; Moya *et al.* 2015; Vargas *et al.* 2018; Solari *et al.* 2006; Novillo and Ojeda 2014). More detailed and precise information is required, in order for the relationship between diversity and elevational gradients, and ecology and biogeography of small non-flying mammals, to be better understood.

Recent various reports combined metacommunity structure with studies on biodiversity gradients along multiple dimensions of biodiversity --from taxonomic and phylogenetic to functional -- in the tropical Andes (Presley *et al.* 2012; Dreiss *et al.* 2015; Willig and Presley 2016). These studies suggest that communities of small non-flying mammals were composed of habitat specialists (Presley *et al.* 2012), and that changes in composition were always associated with ecotones between major ecological zone (Willig and Presley 2016). Dreiss *et al.* (2015) found that species richness was highly correlated with phylogenetic biodiversity, and this with functional biodiversity. They also found that richness was better explained by high vertical vegetation complexity and high productivity of rainforests.

The eastern escarpments of the Andes range from 800 and more than 6,000 masl and are marked by complex topography and steep slopes, which in combination generate a very complex mosaic of plant formations and a great diversity of species (Beck 1988; Ribera-Arismendi 1995).

Small mammal richness in Bolivia is well-recognized (Anderson 1997; Salazar-Bravo *et al.* 2002, 2003; Wallace *et al.* 2010; Aguirre *et al.* 2019), and it continues to increase year by year. The mammalian fauna of the region is relatively well known (Villalpando 2004; Solari 2007; Mena *et al.* 2011; Vargas *et al.* 2018; Identidad Madidi and SERNAP 2019, among others), comparatively little is known about the ecology or the patterns of co-occurrence and interactions among the species present on the region (Dreiss *et al.* 2015). The goal of this study was to determine the pattern of richness and composition of small non-flying mammal communities along an altitudinal gradient in Cotapata National Park, as well as to evaluate the responses of these species to this gradient in elevation.

Methods

Study area. This study was conducted in the Cotapata National Park and Integrated Management Natural Area (PN ANMI, -16° S and -68° W, Cotapata hereon) located NE of the city of La Paz, on the eastern slope of the Eastern Cordillera, in the Yungas Biogeographic Sector (Navarro and Maldonado 2002; Sevilla-Callejo and Mata-Olmo 2007). Cotapata has an estimated area of 56,620 ha, but due to the irregularity of the relief, it could cover an area of more than 80,000 ha. The area ranges from 1,100 to 5,600 masl (Ribera-Arismendi 1995; Sevilla-Callejo and Mata-Olmo 2007; Figure 1). Altitudinally, it covers six ecological zones: Nival (above 5,000 masl), Subnival, High Andean, Yungas Paramo, Yungas Cloud Forest (mountain ridge), and Yungas mountain rain forest (1,100 masl; Ribera-Arismendi 1995). It presents two main climate types: polar of high mountain and humid mesothermic with summer rains and dry and warm winters (Cloud Forest and Yungas Forest; Ribera-Arismendi 1995), generating a dry and humid season.

The fieldwork was done to cover the greatest possible altitudinal extension, covering the last three ecological floors, with an altitudinal range from 1,200 masl (Yungas Forest) to 4,200 masl (Yungas Paramo). The inferior floor is the Yungas Forest that goes from the 1,200 to 2,400 msnm, with humid subtropical climate, annual precipitation less than 2,000 mm and temperatures between 12 and 17 °C. It presents a greater seasonality, with a marked dry season between June and September (Ribera-Arismendi 1995). It is located on steep slopes, in relatively wide alluvial valleys and deep gorges. The forest on this floor is of medium height, where the upper stratum is dense and continuous between 15 and 20 m, with emergents of up to 30 m (*Ficus* spp., *Aniba* spp.) and the lower strata are very dense (Ribera-Arismendi 1995). It is followed by the Cloud Forest that extends from 2,200 to 2,300 to 3,300 to 3,500 masl and whose topography is made up of ridges, hilltops, and very steep and deep gorge slopes, where its slopes have a strong exposure to humid air masses (Ribera-Arismendi 1995). The climate is predominantly cold and perhumid, characterized by frequent rain and orographic drizzle, with an influx of wetting fog (horizontal rain) throughout the year. Rainfall exceeds 3,000 mm per year. Seasonality is diffuse, with drier periods between August and September (Ribera-Arismendi 1995). The forest on this floor has a canopy height between 10 and 15 m on average, with scattered emergence of *Miconia theaenazas* of up to 30 m. The lower stratum is very dense and rich in lianas, tangle of bamboo *Chusquea* spp. and lianescent shrubs; as well as ferns, bromeliads, and orchids (Ribera-Arismendi 1995). The floor of Yungas Paramo is located between 3,300 and 4,200 masl. The weather is dominated by high humidity (drizzles and wetting fogs almost all year round) hyperhumidity (soil generally saturated with water) with annual rainfall above 1,400 mm, and a short dry period between August and September. Average daily temperatures are less than 10°C (Ribera-Arismendi 1995). This area generally extends over mountain peaks and plateaus that are surrounded by the cloud forests of the surrounding valleys. This floor is covered by a thick layer of organic matter and humus of the Mor type, where mosses, lichens (*Cora pavinona*) and fungi grow, alternating with a rich flora of low growing camephites (*Perezia* spp, *Hypochoeris* spp., *Liabum ovatum* spp., among others) and small dispersed stands of *Polylepis pepei* queñua, *mountain Buddleja* (Kishuara) shrubs and *Bacharis pentlandii* forests (Ribera-Arismendi 1995).

Sampling. The sampling was conducted on the gradient between 1,200 and 3,600 masl (Figure 1), and from 2007 to 2009. Due to accessibility and the steep slopes, three altitudinal surveys were conducted, which co-incide with the three lower ecological floors of the National Park. Thus, Chairo (1,200 to 1,600 masl) was selected to represent the Yungas Forest (lower sampling margin is provided by the Huarinilla River; Figure 1). The locality of Alto Nogalani (2,100 to 2,300 masl) was selected as one representing the ecological floor of the Cloud Forest unit. Finally, the plateau of Hichuloma (3,400 to 3,600 masl) that sampled as a representative of the Yungas Paramo. With the exception of Alto Nogalani, which presents some plots of family crops (which were not part of the sampling), the remainder of the study sites have very little human intervention. Six temporal replicates, of seven nights of sampling each, were conducted in the study sites: July 2007 (dry season), September 2007 (dry-wet transition), February 2008 (wet season), August 2008 (dry season), October 2008 (dry-wet transition), and April 2009 (wet-dry transition); in the latter, sampling could not be conducted at the altitude of 3,600 meters above sea level. Three linear transects each of ca. 250m, were placed at each elevation. Each transect had 25 sampling stations (with two snap traps: a *special Museum* and a *Victor* trap) separated by 10 meters. The traps were baited with a mixture of tuna, oats and vanilla essence (Santos *et al.* 2007; Luévano *et al.* 2008; Cruz et *al.* 2010) and checked early in the morning. Additionally, to have a better record of the richness of each site, in the Yungas Forest and the Cloud Forest, three and two transects of pitfall barrier traps were placed, respectively. Each pitfall trap transect had five buckets (25 cm in diameter) separated by 5 m. In the Yungas Paramo they were not placed due to the rocky structure of the soil. At all sampling sites, traps were set for seven consecutive nights, for a total of 17,850 night traps and 1,050 pitfall-nights (Table 1).

Processing of the specimens. All specimens were handled following the guidelines of the American Society of Mammalogy (*ad hoc* Committee on Acceptable Field Methods in Mammalogy 1998; Gannon *et al.* 2007) and were processed in the field. Standard measurements, gender, and reproductive status were obtained recorded for all specimens (Santos *et al.* 2007). Specimens were identified according to Anderson (1997), Patton *et al.* (2000), Salazar-Bravo et al. (2002), Salazar-Bravo *et al.* (2003), Voss *et al.* (2004), Villalpando *et al.* (2006), Weksler *et al.* (2006),

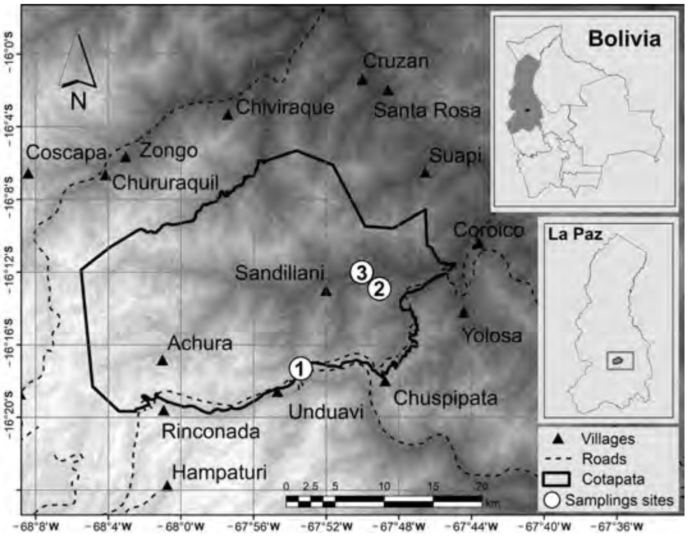

Figure 1. Geographical location of the Cotapata National Park and Integrated Management Area. Sampling sites: 1 Hichuloma-Unduavi Plateau (3,400 - 3,600 masl); 2: Alto Nogalani (2,100 - 2,300 nsnm); 3: Chairo (1,200 - 1,600 masl).

Patton *et al.* (2015), Hurtado and Pacheco (2017), among others, and reference specimens from the Bolivian Collection of Fauna (CBF).

Data analysis. Capture effort was estimated by multiplying the number of traps used each night by the number of nights traps were deployed (trap-nights). The relative abundance was obtained from the capture effort. Species accumulation curves (Chao 1 and Chao 2) were used to estimate the representativeness of the sampling in each of the ecological zones. The Chao 1 estimator considers abundance, while the Chao 2 estimator is based on species incidence (Escalante 2003). Although it was not possible to sample Yungas Paramo in 2009, overall the sampling effort was homogeneous within each altitudinal floor; therefore, the results are considered comparable across sites and years. Individuals collected in pitfall traps were considered only for the calculation of relative abundance, since preliminary analyses showed no differences with diversity, but they are important for the richness data. Species richness (*S*) considered as the number of species and absolute abundance (total number of individuals of all species) were estimated per ecological zone. Diversity and equitability (ranging from 0 to 1) were estimated using Simpson's inverse index (*Cinv*; Begon *et al.* 2006) which is a better indicator when working with small populations as it is less sensitive to rare species (Begon *et al.* 2006). Alpha diversity was calculated by combining results of all temporal replications, for all species, at each of the three sampled ecological zones. Gamma diversity was estimated by combining species records at each elevation. To determine if there are significant differences in relative abundance and diversity among the three ecological floors sampled, we used Kruskal-Wallis test, because the data did not meet the assumption of normality (Zar 2010). To determine the differences between pairs of ecological zones we used U Mann-Whitney (with Bonferroni correction) using the SPSS v19 statistical package (Norušis and SPSS Inc. 1990). Since diversity is an index that does not show species composition, rank–abundance curves were plotted to determine differences in species composition and abundance at each ecological zone. Finally, we used the Morisita-Horn quantitative similarity coefficient in PAST v 4 03 statistical package (Hammer *et al.* 2001), to determine the similarity in species composition among the three floors: Yungas Paramo, Cloud Forest and Yungas Forest.

Results

We captured 460 specimens, corresponding to 20 species of the order Rodentia (96.74 % abundance) and two of the order Didelphimorphia. Of these, 402 specimens were captured with snap traps and 58 in pitfall (Table 1). The number of species found per ecological zone (each elevation sampled) throughout the study period varied from 2 to 10, and the number of animals captured varied from 11 to 53 (Table 1). The most abundant species was *Akodon mimus* with more than 25 % of the individuals captured, although it was captured only in the Yungas Paramo (Table 3). It was followed in abundance by *Akodon baliolus, Nephelomys levipes* and *Neacomys vargasllosai,* with abundances between 10 and 15 % (Table 2). Less abundant (3 to 7 %) were *Oligoryzomys occidentalis*, *Oligoryzomys destructor*, *Microryzomys minutus* and the marsupial *Marmosops noctivagus* (Table 2), followed by *Thomasomys* sp1, *Oecomys phaeotis* and *Oxymycterus nigrifrons* (with just over 1 %). The remainder of the species collected (n = 11) did not exceed 1 % and were thus considered rare species (Table 2).

The relative abundance of the set of temporary replicates did not vary between the elevations ($H = 3.12$, $n = 26$, $P = 2.11$), although the Yungas Paramo ($n = 199$, $S = 8$, $Cinv = 2.12$) presented a greater relative abundance than the Cloud Forest ($n = 134$, $S = 9$, $Cinv = 3.32$) and this in turn, more than the Yungas Forest ($n = 69$, $S = 9$, $Cinv = 2.85$; Table 1). Species accumulation curves per ecological zone plateaud in species richness before the end of the study

Table 1. Capture effort (snap traps, pitfall) along transects for each elevation with their seasonal replicas, including the species richness and number of individuals captured. Altitudinal range: Yungas Forest 1250-1600 masl; Cloud Forest: 2100-1600 mnsnm; Yungas Paramo: 3450-3550 masl. Capture effort: Yungas Forest 1050 traps/night and 105 pitfall/night; Cloud Forest: 1050 traps/night and 70 pitfall/night; Yungas Paramo: 1050 traps/night and no pitfall. D: Dry season; W: Wet season; D-W: Transition from dry to wet; W-D: Transition from wet to dry.

Elevation	Year	Capture effort	Both methods		Snap traps		Pitfall	
		Season	# sp	# Indiv	# sp	# Indiv	# sp	# Indiv
1,400 masl (Yungas Forest)	2007	D: jul	4	11	4	11	0	0
		D-W: sep	6	23	5	19	4	4
		W: dec-7-feb 8	6	13	5	8	3	5
	2008	D: ago	2	11	2	10	1	1
		D-W: oct	7	31	5	12	5	19
	2009	W-D: apr	2	11	2	9	1	2
Sub total			9	100	9	69	6	31
2,100 masl (Cloud Forst)	2007	D: jul	5	24	5	24	0	0
		D-W: sep	10	47	7	39	6	8
		W: dec-7-feb 8	5	22	3	17	3	5
	2008	D: ago	6	14	6	14	0	0
		D-W: oct	7	30	4	21	5	9
	2009	W-D: apr	6	24	6	19	3	5
Sub total			11	161	9	134	7	27
3,500 masl (Yungas Paramo)	2007	D: jul	5	42	5	42	-	-
		D-W: sep	6	27	6	27	-	-
		W: dec-7-feb 8	6	28	6	28	-	-
		D: ago	4	53	4	53	-	-
	2008	D-W: oct	6	49	6	49	-	-
Sub total			8	199	8	199	-	-
Total			22	460	20	402	9	58

period (Figure 2). Thus, each elevation was considered adequately sampled to evaluate the differences in species richness and composition among the three elevations (ecological zones). The estimated number of species at each elevation, according to the Chao 1 and 2 estimators, are nine species for Yungas Forest, 11 for Cloud Forest, and approximately nine species for Yungas Paramo (one more than the observed observed).

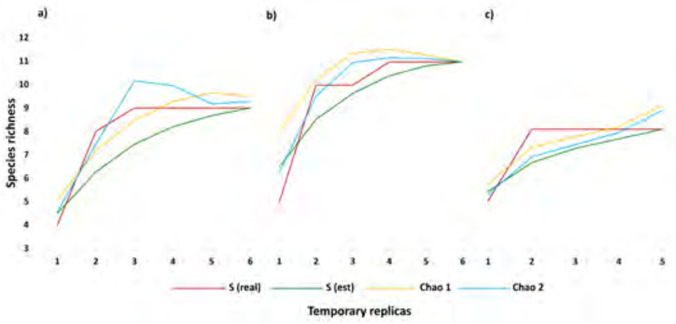

Figure 2. Species accumulation curves for the three elevations (ecological zone) evaluated. a) 1,400 masl (Yungas Forest); b) 2,100 masl (Cloud Forest; c) 3,500 masl (Yungas Paramo). X axis: 1: Dry Season: July 2007. 2: Dry-Wet Season: September 2007; 3: Wet Season: December-2007-February 2008; 4: Dry Season: August 2008; 5: Dry-Wet Season: October 2009; 6: Wet-Dry Season: April 2009. Y axis: Number of species. S (real): real richness; S (est): estimated richness.

The species richness (per temporal replications), while showing seasonal variations (Figure 3a), all peaked at mean elevation (i.e., Cloud Forest), except for the wet season of 2007-2008; however, the differences were not significant (*S* = 9, *H* = 1.29, *n* = 17, *P* = 0.5; Table 2). Species diversity and species richness showed similar patterns (Figure 3b). As in the case of richness, the diversity of the 2007-2008 wet season differed from the remainder of the seasons and is the only one that presents a decrease as elevation increases (Figure 3b). Unlike richness, diversity did present significant differences overall (*H* = 7.0, *n* = 17, *P* = 0.03; Table 2), as well as between the Cloud Forest and the Yungas Paramo (*U* = 0.00, *n* = 11, *P* = 0.004). Other two-pair comparisons showed no significant variations in species diversity: Yungas Forest vs Cloud Forest, *U* = 9, *n* = 12, *P* = 0.18, and Yungas Forest -vs Yungas Paramo, *U* = 10, *n* = 11, *P* = 0.43, even though the latter two did not share even a single species (Table 2).

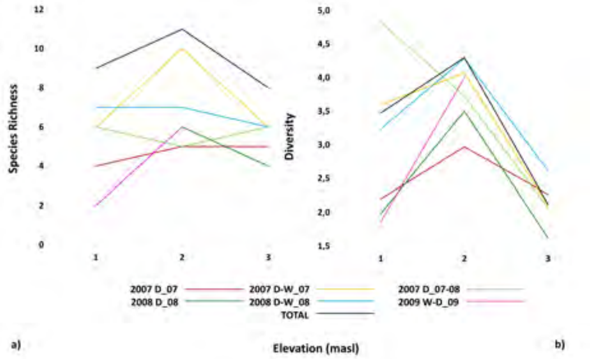

Figure 3. Patterns of a) richness (*S*) and b) diversity (*Cinv*) of species for the six temporal replicas. The combined pattern of species richness and diversity. X axis: 1: 1,400 masl (Yungas Forest); 2,100 masl (Cloud Forest); 3: 3,500 masl (Yungas Paramo). Legend: D_07: Dry Season: July 2007; D-W_07: Dry-Wet Season: September 2007; D_07-08: Wet Season: December-2007- February 2008; D_08: Dry Season: August 2008; D-W_08: Dry-Wet Season: October 2008; W-D_09:. Wet -Dry Season: April 2009; Total: includes all species recorded at any given.

Species composition varied among ecological zones (i.e., high beta diversity), especially between the Yungas Paramo and the other two zones (Figure 4). Thus, the Morisita-Horn Index presents a similarity of 0.54 between the lower levels (Yugas Forest and Cloud Forest), and a similarity of only 0.2 between the Cloud Forest and the Yungas Paramo. Beta diversity was maximum between Yungas Forest and Yungas Paramo as these share no species in common (Figure 4). When considering the composition of the species present at each elevation, there was almost 100% change in the species between the lower levels and the Yungas Paramo (Figure 5). The Yungas Forest and the Cloud Forest share 5 of 15 species, *Akodon baliolus*, *Neacomys vargasllosai*, *Oligoryzomys destructor*, *Marmosops noctivagus* and *Akodon cf. kofordi* (from highest to lowest abundance; Table 2, Figure 5). Only *Oligoryzomys occidentalis* occurs in both Cloud Forest and the Yungas Paramo, being more abundant in the latter (Table 2, Figures 5); while no species are shared between the Yungas Paramo and the Yungas Forest (Table 2, Figure 5).

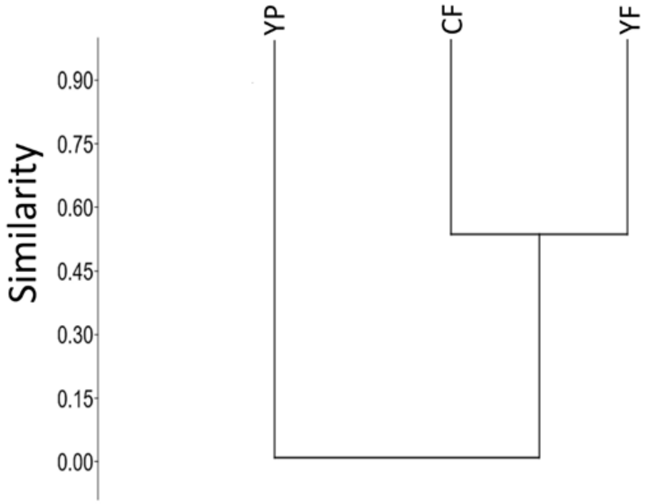

Figure 4. Clustering analysis of the three ecological floors, according to the Morisita-Horn quantitative similarity index. YF: 1,200 masl-Yungas Forest; CF: 2,100 masl-Cloud Forest; YP: 3,500 masl- Yungas Paramo.

The Cloud Forest (intermediate elevation site) was the ecological floor with the highest alpha species richness and diversity (Table 2). Although it was not the most abundant site, it presented relatively high equitability, with several relatively abundant species and few rare species. The species registered as exclusive to this floor were *Nephelomys levipes*, *Rhagomys longilingua*, *Thomasomys* sp. 2, *Lenoxus apicalis* and *Cavia aperea nana* (Figure 5b). The Yungas Forest is still rich in alpha diversity, but was the least abundant forest floor; it presented a slightly lower equitability than the Cloud Forest, due to the dominance of *Neacomys vargasllosai* and *Akodon baliolus* (Table 2), and the presence of three exclusive species: *Hylaeamys yunganus, Rhipidomys austrinus* and one species of the genus *Proechimys* (Figure 5a). The Yungas Paramo was the floor with the least richness and alpha diversity, but where the total number of specimens captured was highest. It also showed the least equitability, due to the dominance and great abundance

Table 2. Number of collected individuals by species and altitudinal floor, richness (*S*), diversity (*Cinv*) and equitativity (*E*). * Species that were collected only in pitfall. YF: 1,200 masl-Yungas Forest; CF: 2,100 masl-Cloud Forest; YP: 3,500 masl- Yungas Paramo. Total: Sum of the total number of individuals on each floor.

Classification		Ecological floor				%
Family	Specie	YF	CF	YP	Total	from total
Cricetidae	*Akodon baliolus*	37	34	0	**71**	15.43
	Akodon cf. kofordi	1	1	0	2	0.43
	Akodon mimus	0	0	132	**132**	28.70
	Lenoxus apicalis	0	2	0	2	0.43
	Oxymycterus nigrifrons	0	0	7	7	1.52
	Hylaeamys yunganus	2	0	0	2	0.43
	Microryzomys minutus	0	0	17	17	3.70
	Neacomys vargasllosai	37	23	0	**60**	13.04
	Nephelomys levipes	0	63	0	**63**	13.70
	Oecomys phaeotys	8	0	0	8	1.74
	Oligoryzomys destructor	6	15	0	21	4.57
	Oligoryzomys occidentalis	0	7	29	36	7.83
	Phyllotis osilae phaeus	0	0	3	3	0.65
	*Rhagomys longilingua**	0	2	0	2	0.43
	Rhipidomys austrinus	3	0	0	3	0.65
	Thomasomys ladewi	0	0	1	1	0.22
	Thomasomys sp 1	0	0	9	9	1.96
	Thomasomys sp 2 *	0	2	0	2	0.43
Caviidae	*Cavia aperea nana*	0	3	0	3	0.65
Echimyidae	*Proechimys* sp.	1	0	0	1	0.22
Didelphidae	*Marmosops noctivagus*	5	9	0	14	3.04
	Gracilinanus aceramarcae	0	0	1	1	0.22
Total abundance		100	161	199	460	100
Richness (*S*)		9	11	8	22	
Diversity (*Cinv*)		3.47	4.30	2.12	1.218	
Equitativiity (*E*)		0.386	0.391	0.265	0.55	

of *Akodon mimus,* > 130 individuals (Table 2). The largest number and proportion of exclusive species was found on this floor, with seven of its eight species: *A. mimus*, *Microryzomys minutus*, *Oxymycterus nigrifrons*, *Phyllotis osilae phaeus*, *Thomasomys ladewi*, *Thomasomys* sp.1 and *Gracilinanus aceramarcae* (Figure 5c).

Discussion and conclusions

In this work, we concentrated our efforts on three of the five ecological zones present along the steep elevation gradient present in the area: we did not sampled Subnival and Nival floors. Sampling was conducted at three elevations, looking for coincidence with the marked ecological zones present in the Yungas zone (Ribera-Arismendi 1995). Although we found that species richness was greatest at middle elevations (Cloud Forest), we found that species richness (number of species) did not vary significantly across ecological zones, but species diversity did. On both cases, our results show a positive monoclinal hump-shaped pattern, where richness and diversity are greater at half of the maximum elevation. This is the pattern predicted by the mean dominance effect (McCain 2005; Currie and Kerr 2008) but see Colwell and Hurtt (1994) and Colwell and Lees (2000), for alternative interpretations. Richness and composition appear to closely track habitat diversity at each ecological floor as has been reported previously (Rahbek 1995; McCain 2005; Körner 2007; Novillo and Ojeda 2014; Brown 2001; Lomolino 2001; McCain 2004). Therefore, the maximum richness should be produced in a point where the environmental conditions are optimal (high productivity and structural diversity) and in the zone of rapid transition between different vegetation communities (Lomolino 2001; Willig and Presley 2016), which in our case would correspond to the Cloud Forest.

Patterson *et al.* (1998) and Solari *et al.* (2006) found a decline in the biodiversity of small non-flying mammals

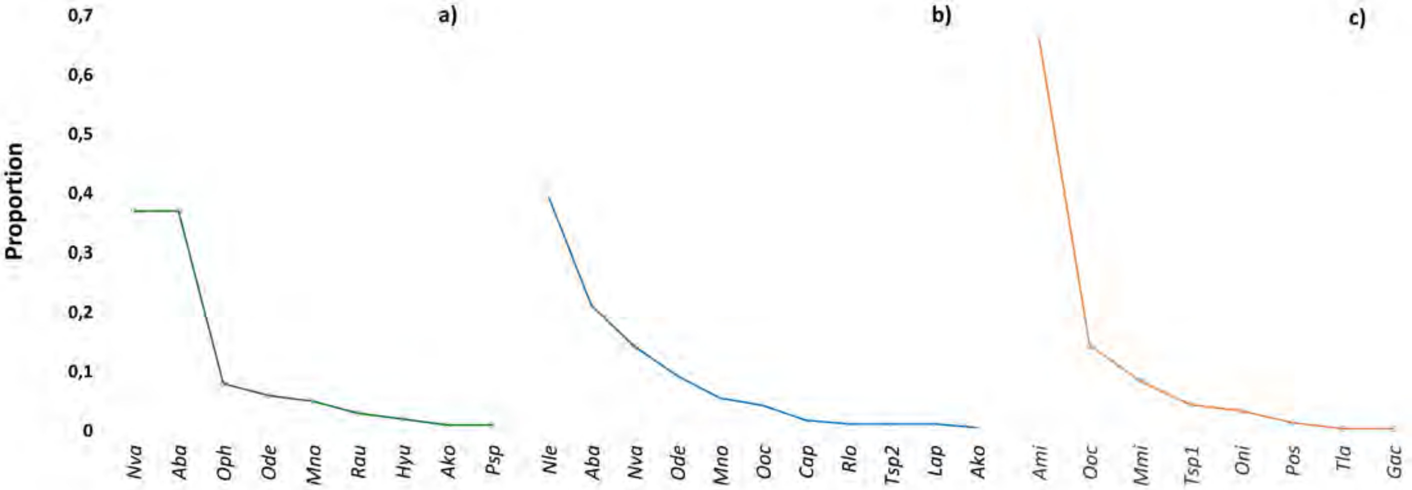

Figure 5. Abundance range curve for each of the elevational floors. Ami = *A. mimus*; Aba = *A. baliolus*; Ako = *A. cf. kofordi*; Cap = *C. aperea nana*; Gac = *G. aceramarcae*; Hyu = *H. yunganus*; Lap = i; Mmi = *M. minutus*; Mno = *M. noctivagus*; Nle = *N. levipes*; Nva = *N. vargasllosai*; Ode = *O. destructor*; Ooc = *O. occidentalis*; Oph = *O. phaeotis*; Oni = *O. nigrifrons*; Pos = *P. osilae phaeus*; Psp = *Proechimys* sp.; Rau = *R. austrinus*; Rlo = *R. longilingua*; Tla = T. *ladewi*; Tsp1 = *Thomasomys* sp 1; Tsp 2 = *Thomasomys* sp 2.

in Manu National Park and Biosphere Reserve (Perú) as elevation increased. A similar pattern was observed by Vivar (2006) in the Yanachaga mountain range (Perú). However, Patterson *et al.* (1998) and Vivar (2006), when conducting the analysis for cricetid rodents only, observed that there was a greater species richness at the ends of the curve (inverse monoclinal). According to Dreiss *et al.* (2015), all these patterns are explained by the vertical complexity of the vegetation and the higher productivity of rainforests when compared to mountain forests (at higher elevations). In addition, inhospitable and stressful conditions generate physiological restrictions and a competitive exclusion in favor of certain better-adapted clades of cricetid rodents (Mena *et al.* 2011). In our case, we found greater richness and diversity in the Cloud forest, which would correspond to the cloud forest of Manu and Yanachaga (lower richness). These results do not contradict each other, since for the Cotapata National Park area, the ecological zone of the Cloud Forest has a greater structure in the vegetation (Ribera-Arismendi 1995) providing a greater diversity of niches.

In addition, due to the accessibility issues and the steep slopes in Cotapata National Park, our sampling concentrated near transition zones, between Yungas Forest and Cloud Forest (2,000 to 2,400 masl), and between Cloud Forest and Yungas Paramo (3,000 to 3,300 masl), which can be considered peak diversity zones as they mark the transition between these communities (Lomolino 2001). The degree of shared species, and therefore the composition and abundance of species, in and between sampling sites, depends on spatial heterogeneity and extension (Pielou 1966; Whittaker 1977; Chaneton and Facelli 1991; Hill and Hamer 2004); that is, local conditions such as type of vegetation and associated food resources (Brown *et al.* 2001). We observe greater diversity and richness at the lower limit of the Cloud Forest, between 2,300 and 2,400 masl, with greater mixing and overlapping of ranges in both directions; while at 3,400 masl, the contribution of higher altitude zones would be less (Lomolino 2001). This is something that should be corroborated with a greater number of sampling points within the ecological floors.

Although the vegetation in the Cloud Forest is structurally more complex than in the Yungas Forest, they share a large number of environmental characteristics, providing a great variety of food and shelter resources. So, the similarity in species composition, especially the presence of the same abundant species (*Neacomys vargasllosai* and *Akodon baliolus*) and the observed replacement (5 of 15 species) can be explained by the structural complexity. But, also by habitat preference and/or adaptability of each species, where some will be generalists (such as *Neacomys vargasllosai*, *Akodon baliolus, Oligoryzomys destructor,* shared and abundant) and other specialists, in relation to the site resources (such as *Nephelomys levipes,* abundant but exclusive to the Cloud Forest; Willig and Sandlin 1992; Cruz *et al.* 2010).

Similarly, the above conditions may be responsible for the variation in species richness and composition between the Cloud Forest and the Yungas Paramo. However, other factors must be influencing the reduction in richness and the almost total change of species, which go beyond the climatic conditions. According to Lomolino (2001) as one moves to higher elevations, populations would become more isolated; therefore, immigration rates should decrease and local population extinction rates should increase (Brown and Kodric-Brown 1977). This would explain the lower number of species; but also, and precisely because of this isolation, higher elevation areas may provide the geographic isolation required for speciation (Heaney 2001; Rahbek 1995). It has been suggested the Andes have played a very important role in the speciation of sigmodontine rodents (Reig 1986; Patton and Smith 1992). On the other hand, conditions such as low partial oxygen pressure and low environmental temperatures, present at higher elevations, are a challenge for endothermic species; species living at these altitudes must present certain physiological adaptations to hypoxia, lower temperature, and lower baro-

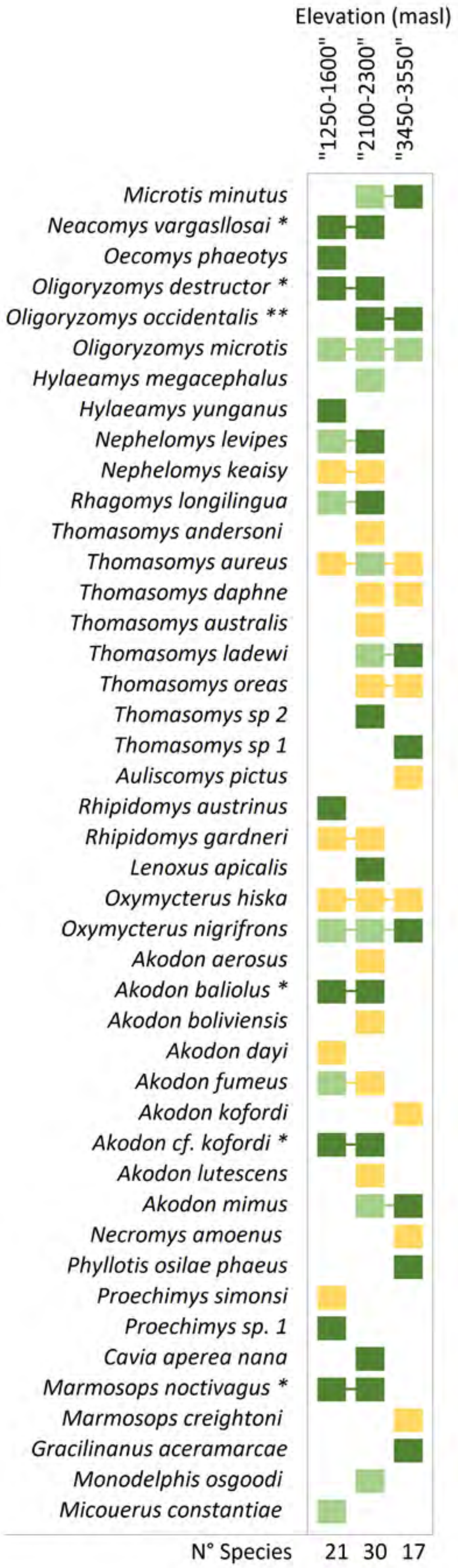

Figure 6. Elevation ranges of each documented species along the sampling transects of this work and according to the literature for the sampling site. Dark-green squares indicate places where the individuals were collected in the present work; the light green squares, in the work of Villalpando (2004) and the yellow squares according to literature. * Species shared between Yungas Forest (YF) and Cloud Forest (CF); ** Species shared between Cloud Forest (CF) and Yungas Paramo (YP).

metric pressure (Mena *et al.* 2011). Thus, the almost complete replacement of species recorded between the Cloud Forest and the Yungas Paramo may, in part, be explained by an ecological filter.

McCain (2009) indicates that species turnover and altitudinal distribution are not only related to changes in climatic conditions (temperature as elevation increases), but also to the latitudinal position of mountains. Thus, in higher latitudinal ranges, the overlap of species along the altitudinal gradient is greater. While at lower latitudes (as in our case), the overlap is less and species turnover is more evident (McCain 2009). This is primarily due to a smaller range of climate variation throughout the day, but also throughout the year (McCain 2009). In our work we can show that, for the eastern slope of the Eastern Cordillera of the Cotapata National Park, for small non-flying mammals, not only is there greater species richness at intermediate elevations (McCain 2005), but the altitudinal range of the species collected is relatively narrow, mainly in the species found at higher elevations, following McCain (2009) prediction.

The pool of potential species in the study zone is deep. A quick review of the literature indicated that several species are expected to occur on our study site but that were not found despite intensive sampling. Among the species reported for the Yungas Paramo zone are eight species: *Thomasomys aureus, T. daphne, T. oreas* (Anderson 1997; Pacheco 2015), *Necromys amoenus* (Salazar-Bravo *et al.* 2002; Pardiñas *et al.* 2015a), *Akodon kofordi* (Salazar-Bravo *et al.* 2002; Pardiñas *et al.* 2015b), *Oxymycterus hiska* (de Oliveira and Gonçalves 2015), *Auliscomys pictus* (Salazar-Bravo 2015; Vargas *et al.* 2018), *Marmosops creightoni* (Voss *et al.* 2004). For the Cloud Forest there are an additional 16 species: *Akodon aerosus, A. boliviensis, A. fumeus, A. lutescens,* (Anderson 1997; Pardiñas *et al.* 2015b; Vargas *et al.* 2018), *Oxymycterus hiska, O. nigrifrons, O. paramensis* (Villalpando 2004; de Oliveira and Gonçalves 2015), *Thomasomys andersoni* (Salazar-Bravo and Yates 2007; Pacheco 2015), *T. australis, T. ladewi, T. aureus, T. daphne, T. oreas* (Anderson 1997; Villalpando 2004; Pacheco 2015), *Nephelomys keaysi* (Percequillo 2015), *Rhipidomys gardneri* (Tribe 2015; Aguirre *et al.* 2019), *Monodelphis osgoodi* (Villalpando 2004). Lastly, for Yungas Forest, 8 species: *Akodon dayi* (Anderson 1997; Pardiñas *et al.* 2015b), *A. fumeus* (Anderson 1997; Villalpando 2004; Pardiñas *et al.* 2015b; Vargas *et al.* 2018), *O. hiska* (de Oliveira and Gonçalves 2015), *T. aureus* (Anderson 199; Pacheco 2015), *N. keaysi* (Percequillo 2015), *R. gardneri* (Tribe 2015), *Proechimys simonsi* (Patton and Leite 2015), and *Micoureus constantiae* (Villalpando 2004; Figure 6).

We restricted our considerable sampling effort to narrow belts of elevation that correspond to major ecological zones. As such, it is possible that that our sampling just failed to include the ribbon-like distributions of several of these potential species. In addition, although our sampling regime was designed to sample a wide range of habitats in each of our sampling units (ecological zones), it is likely that we missed some (or various) of the most restricted habitat types. Then, it is not surprising that many rare or "specialists" species may have been missed. In addition, although our experimental design included two snap traps per sampling station, it may be necessary to up the trapping effort register rare species, especially in those sites where one or a few species are common to very abundant, such as is the case of *A. mimus* in Yungas Paramo.

Although this paper does not attempt to analyze the distribution patterns of small non-flying mammals, it is important to highlight the similarities in the altitudinal distribution of the most diverse groups found in this study, which coincide with the work done by Patton (1986) on the eastern slopes of the Peruvian Andes. As in his work, it was evident that there are genera that are restricted only to certain altitudinal ranges, as in the case of *Phyllotis* or *Thomasomys,* while others, such as *Akodon*, *Oligoryzomys* and *Oxymycterus,* present a survey of species along the gradient.

The general results presented herein challenge the common-held idea that there is a decline of species diversity with increase elevation. Instead, our work indicates that the patterns predicted by McCain (2009) are maintained, even if one includes species that were not collected at the study site, but are found in these altitudinal ranges (Figure 7). In general, the combination of these results indicate that potential species pools, historical origin of clades, and diversification rates (Quintero and Jetz 2018), among other variables, are important at the moment of explaining local and regional diversity gradients (Montaño-Centellas *et al.* 2019). This is the first of a series of papers assessing the distribution of small, non-flying mammals along the steep elevational range of the Bolivian Yungas and much more detailed analysis, with data of greater altitudinal and longitudinal amplitude, will be forthcoming.

The Andes present two cordilleras running on an approximate N-S direction in Bolivia, each with similar geological histories, but exposed to very dissimilar ecological and environmental forces and a different pool of potential species of mammals. We urge the continuous effort of documenting general patterns of species diversity along each of these branches of the Andes, as well as studies that focus on trophic relationships, and that document morphological and categorical features of the resident species. Only then, will we be able to disentangle functional, phylogenetic and taxonomic dimensions of biodiversity and assess how each is apportioned across space and time.

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Bolivian river dolphin site preference in the middle-section of Mamoré River, upper Madeira river basin, Bolivia

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The South American river dolphins of genus *Inia* are distributed throughout the Amazon, Orinoco and Araguaia-Tocantins basins. They are categorized as Endangered and the knowledge on their basic ecology is still scarce. Therefore, investigation efforts must contribute to the knowledge and conservation of these species in their area of distribution. For the Bolivian river dolphin we used a database of 10 years of upstream and downstream surveys, accumulating approximately 6,100 km of double routes from three main rivers of the Upper Madeira River basin (Ibare, Mamoré and Tijamuchi) by following standardized methods where each encounter with a single or a group of river dolphins was registered. Preferred sites by Bolivian river dolphin were based on Kernel density estimation. This methodology considers the accumulated data of georeferenced sightings, generating a map of probability of occurrence in each river. In the three rivers, the accumulated density of sightings is concentrated in meanders and confluences, resulting in a high probability of sighting Bolivian river dolphin in these habitats. It was also identified that the number of Bolivian river dolphin sightings decreased over time in the upper Tijamuchi River. The Bolivian river dolphin preferred both meanders and confluence habitats. Between the Ibare and Tijamuchi rivers (Mamoré sub- basin), the distribution of the species tended to be more uniform. According to these results, it is important to reinforce the management of the Ibare-Mamoré municipal protected area, since important Bolivian river dolphin populations are concentrated there. Same trend was also shown in the lower-middle zone of the Tijamuchi River, suggesting the need of implementing conservation strategies in this area, where currently there are none.

Los delfines de río sudamericanos del género *Inia* se distribuyen por las cuencas del Amazonas, Orinoco y Araguaia-Tocantins, se clasifican como en peligro de extinción y el conocimiento sobre su ecología básica aún es escaso. Por lo tanto, las investigaciones deben contribuir a la conservación y el conocimiento de estas especies en su área de distribución. Para el delfín del río boliviano, utilizamos una base de datos de 10 años de recorridos río aguas-arriba y río aguas-abajo, acumulando aproximadamente 6,100 km de rutas dobles en tres ríos principales en la subcuenca alta del río Madeira (Ibare, Mamoré y Tijamuchi). Siguiendo los métodos estandarizados cada encuentro con uno o un grupo de delfines de río fue registrado. La identificación de los sitios preferidos por los bufeos fue estimada por la densidad del Kernel. Esta metodología considera los datos acumulados de avistamientos georreferenciados que generan un mapa de probabilidad de ocurrencia en cada río. En los tres ríos, la densidad acumulada de avistamientos se concentra en meandros y confluencias, lo que resulta en una alta probabilidad de ver bufeos en estos hábitats. También se determinó que los avistamientos de bufeos han disminuido en la parte superior del río Tijamuchi. Los bufeos prefirieron los hábitats de meandros y de confluencia; entre los ríos Ibare y Tijamuchi (cuenca Mamoré), la distribución de las especies tendió a ser más uniforme. Según estos resultados, es importante reforzar la gestión del área protegida municipal de Ibare-Mamoré, ya que allí se concentran importantes poblaciones de bufeo. La misma tendencia también se mostró en la zona media-baja del río Tijamuchi, lo que sugiere la necesidad de implementar estrategias de conservación en esta área, donde actualmente todavía no se ha declarado ninguna.

Keywords: bufeo; conservation area; kernel density; occurrence probability; preferred pites.

Introduction

South American river dolphins of genus *Inia* (family Iniidae) are distributed throughout the Amazon, the Orinoco and the Araguaia-Tocantins basins (Trujillo *et al.* 2010a; Trujillo *et al.* 2010a). Like most freshwater dolphins, they are categorized as Endangered (da Silva *et al.* 2018). River dolphins are threatened by water pollution, habitat degradation, deforestation, heavy boat traffic, overfishing, the construction of hydroelectric dams, bycatch and directed capture for illegal uses, *e. g.* production of oil used as traditional remedy or as bait for fishes such as blanquillo (*Calophysus macropterus*, *Hypophthalmus* sp.; Reeves and Leatherwood 1994; Aliaga-Rossel and McGuire 2010; Trujillo *et al.* 2010b; Smith *et al.* 2012; Mosquera-Guerra *et al.* 2015).

The family Iniidae is restricted to freshwater environments, occupying the main courses of rivers, lagoons, confluences, and streams. During high water season, they tend to disperse and occupy environments such as flooded forest, small tributary rivers, seasonal isolated lagoons and other aquatic habitats of the flooded-lowlands (Pilleri and Gihr 1977; Best and da Silva 1993; Aliaga-Rossel 2002). Most of the studies focused on *Inia* population estimations and briefly mentioned a habitat preference, with a greater number of encounters in confluence, tributary, and lagoon areas (McGuire and Winemiller 1998; Aliaga-Rossel 2002; Martin and da Silva. 2004a, b; Martin *et al.* 2004; McGuire and Aliaga-Rossel 2007; Gómez-Salazar *et al.* 2011, 2012b; Guizada and Aliaga-Rossel 2016; Trujillo *et al.* 2019).

Although limited, knowledge about habitat use, habitat preferences or occurrence of *Inia* varies according to spatial and temporal scales. The most outstanding studies are those from the long-term (more than 25 years) monitoring project called *Projeto Boto* in the Mamirauá Sustainable Development Reserve (central Amazon), specifically with techniques of photo identification (da Silva and Martin 2000; Martin and da Silva 2004a) and telemetry (Martin and da Silva 2004b).

The Bolivian river dolphin (*Inia boliviensis*) is locally known as "bufeo", which is the only recognized name of these animals in Bolivia. Therefore, throughout this report we use this local name, which contrasts to the term used by the International Whaling Committee (IWC), or 'boto' (Aliaga-Rossel and Guizada 2020). The Bolivian bufeo was declared a national and regional natural heritage, despite of this declarations, the threats over their populations are increasing. In order to contribute to the understanding of habitat preferences of the bufeo in a complex of rivers located in the middle region of the Mamoré River, our study focuses on and analyzes georeferenced encounters with this species based on monitoring efforts conducted between 2008 and 2019.

Materials and Methods

The study area is a complex of rivers in the middle-section of the Mamoré River, upper Madeira River basin, department of Beni, Bolivia. We studied the Ibare (47.9 km), Mamoré (128.3 km) and Tijamuchi (169.4 km) rivers with a total extension of 345.8 km, or approximately 80 km^{2} (Figure 1). The area corresponds to flood plains savannas called Llanos de Moxos. The Mamoré River is a whitewater river of Andean origin, with water typically dark or yellowish-brown color with little transparency, due to the large quantity of suspended sediment (Guyot 1993; Albert and Reis 2011). While Ibare and Tijamuchi are black and clear water tributaries, originating in the flooded forest plains, with few suspended sediments (Guyot 1993; Albert and Reis 2011), both rivers are Mamoré confluents. We defined confluences when two or more bodies of water meet; these are areas on the river where a tributary discharge its water into a main river (Aliaga-Rossel and Guizada 2020). Finally, we defined curves and meanders, which are places where the riverbed is wide and has a higher than average current; usually the water flow is fastest along the outside bend of a meander, and slowest on the inside bend, where bufeos prefer to stay (Albert and Reis 2011; Aliaga-Rossel and Guizada 2020).

During the high water-level season, Ibare and Tijamuchi rivers showed an average width of ~200 m, while during the low water-level season width decreased to approximately half (60 to 70 m). On the other hand, the Mamoré River (one of the most important rivers in Bolivia) showed an average width above 200 m, reaching more than 400 m during the high water-level season. The vegetation along the riverbanks is characteristic of a tropical gallery forest. Much of the region is flooded during the high water season. The average air temperature for the region is 26.5°C. The relative humidity ranges between 64 % in August and 77 % in January and February (Aliaga Rossel *et al.* 2006).

Human settlements predominate along Ibare and Mamoré rivers, while cattle ranching is the most important activity in the Tijamuchi River. Logging and other extractive activities such as fishing, for both subsistence and commercialization, are the main activities in the area. Local human communities use the water courses as main transport in Beni, where boat traffic in the last years has also increased due to tourism activities (Aliaga-Rossel *et al.* 2014).

Bufeo sightings. Bufeo encounters were recorded from 2008 to 2019 using the standardized method of linear transect (for main rivers) and 100 strip-band transect (for tributaries), depending on the width and water levels; these methods are widely used for river dolphin surveys (Aliaga-Rossel 2002; Gómez-Salazar *et al.* 2012b). Sightings covered ~50 km of the Ibare (Ib) River with 14 surveys total, ~130 km of the Mamoré River (Ma) with a total of eight surveys, and ~170 km of the Tijamuchi (Tj) river with eight surveys (30 transect surveys total). For each transect survey, a similar size vessel was used: 15 to 25 m long and 1.5 to 2.5 m of height was the minimum used for the data collection. On each transect there were three or four observers at the bow and one assistant to register bufeo encounters. Observers were responsible for recording each dolphin's sighting time, habitat associated, and its geographical position using GPS. All observations were made when optimal visibility was available, from 7:00 to 17:00, with an approximately one-hour lunch break, when the vessel was stopped until resuming effort.

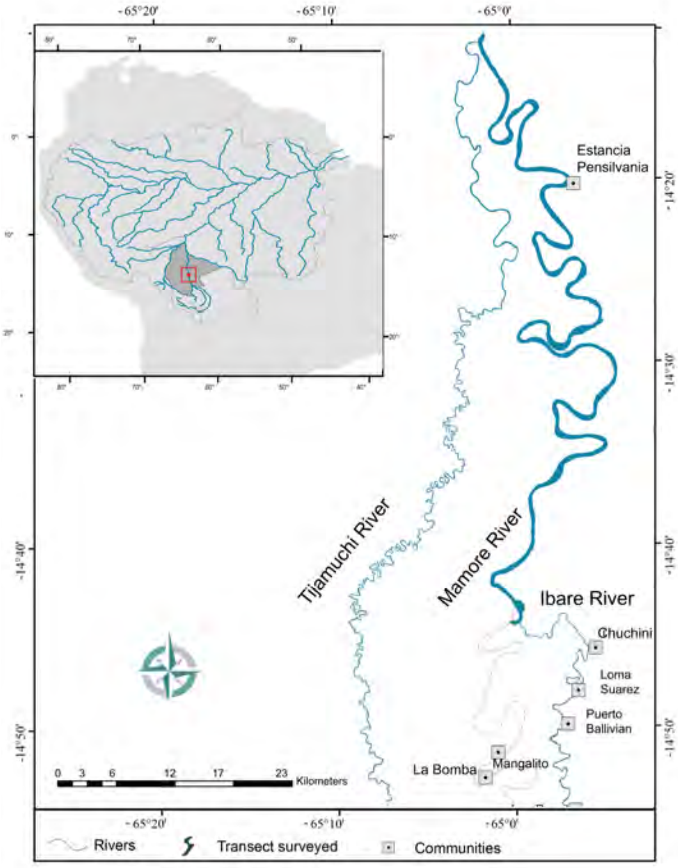

Figure 1. Study site, Ibare, Tijamuchi- Mamoré river complex sampled for river dolphins 2008-2019. Upper Madeira River Basin, Bolivia.

Data analysis. All spatial analyses were performed using ArcGis 10.5 software. For each georeferenced point in a tributary (Ibare and Tijamuchi) a 150 m buffer area was applied, and 200 m to the main Mamoré River. With these polygons, an image per river per year (IRY), with a cell size of 150 m, was created based on the number of bufeos as cell value. For NoData values, they were reclassified to value 0 to perform the raster calculator tool works. All images of each river were added to have a cumulative image. The final image was transformed to a layer of points based on the number of recorded bufeos accumulated along the years in each cell using *raster to point* tool. Kernel Density was applied on the resulting point layer using the quantity parameter registered per cell as *population field*, 150 m as the size cells, and a calculated search radius of 690.9 m corresponding to an area of 1.5 km^2 according to the parameter of average movement of individuals (McGuire and Henningsen 2007).

From the resulting raster, the probabilities of a normal distribution in each cell were obtained to measure the probability of occurrence of bufeos at a given site. The probabilities were calculated with raster package and dependencies on R (R Core Team 2017). After loading the Kernel layer in raster format, the probability values of a normal distribution on the layer were obtained with the *pnorm* function. It was specified that *pnorm* consider the raster mean and twice the standard deviation. Subsequently, the *values function* was used to obtain the values for each cell of a new image. Finally, the *writeRaster* function was used to produce an image with the observation probabilities per cell (script details in appendix 1)

To identify the sites that had constant presence of bufeos over time, IRY raster values were reclassified to absence-presence values (0 to 1) giving an individual condition to each year; which means that if a river had data for four years, the values for each year are 1 (year 1), 10 (year 2), 100 (year 3), and 1000 (year 4). The sum of images per river was performed and the values were reclassified according to the occurrence in number of years, either only one year or several.

Results

The sites that possess the highest density of points of bufeos are meanders and river confluences, clearly represented in maps (Figure 2). Ibare River posesses 47 meanders along the sampled stretch. In only three (6.4 %) of those bufeos have never been registered, and in five (10.6 %) the density of recorded points decreases (spatially not temporarily). The segment of Mamoré River studied possesses 24 river-curves; in all of them, bufeos have been registered. On the other hand, in three (12.5 %) of those the density of occurrence decreased over time. Tijamuchi river has 192 curves; in ten (5.2 %) the density becomes null, and in 37 (19.3 %) the density decreased during time (Figures 2, 3). Based on the density points of bufeo encounters and records, the probability map showed values from 50 % of probability (there may or may not be bufeos there) to higher probability in those places where the density reached 100 %. Finally, accumulative occurrence maps (Figure 3) showed that there are places where bufeos were sighted in a single year of sampling. Nevertheless, there are confluences where bufeos were recorded in more than one year of sampling, and it is interesting to report that Ibare and Tijamuchi rivers presented one and two meanders, respectively, with records in the four years.

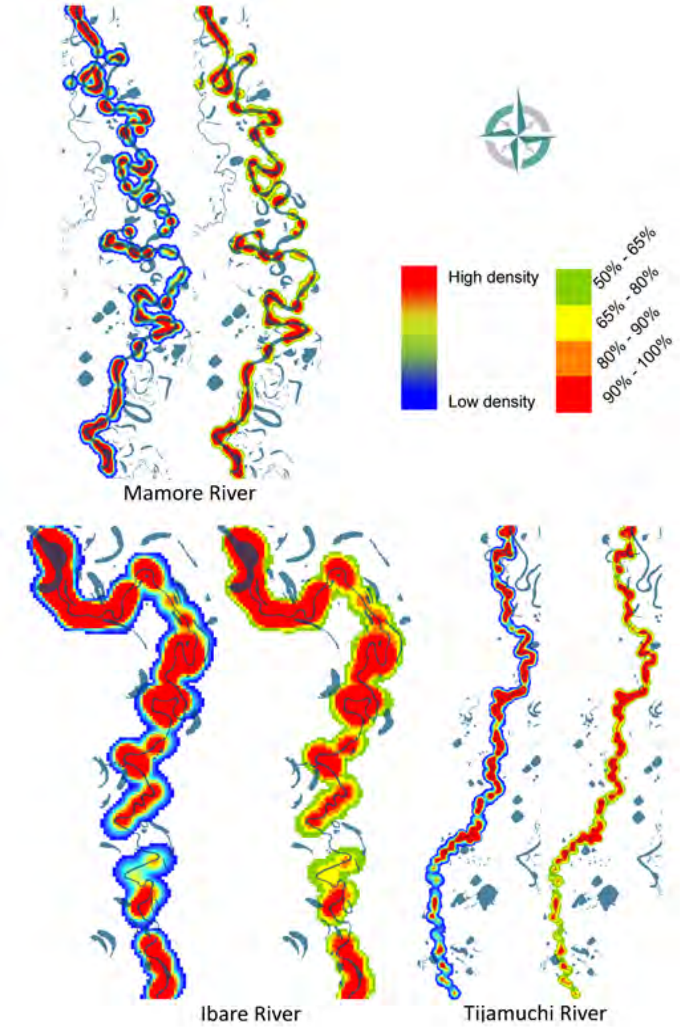

Figure 2. Bufeo presence in the Mamoré, Ibare and Tijamuchi Rivers. Density Kernel Model (left), and Probability of occurrence (right). The three sets of models are not drawn to scale.

Discussion

Analysis of georeferenced data maps from the accumulated average of five years (seven years for Ibare and four for both Mamoré and Tijamuchi) supports the hypothesis that high density of accumulated bufeos (for all years) coincides with two types of habitats: 1) meanders or curves along the main river course, and 2) confluences. This distribution might be explained by sections characterized by the slow river flow in both habitats (Martin and da Silva 2004b). These habitats are preferred not only for being not high energy-consuming for the bufeos, but also for fish's preference for them (Martin and da Silva 2004b). Confluences have been suggested as areas of high productivity for freshwater dolphins in South America (McGuire and Winemiller 1998) and in Asia

(Timilsina *et al.* 2003), housing a high density of fishes, since they provide deep-water environments and shelter (Martin *et al.* 2004; Gómez-Salazar *et al.* 2012a; Mosquera-Guerra *et al.* 2015; Trujillo *et al.* 2019). Also, low-current sites, such as meanders, generally present floating plants that also provide ideal habitat for small fish such as cichlids and catfish (Crampton 1999); these fishes are consumed by bufeos at a much lower energy-cost than in areas with stronger currents. La Manna *et al.* (2016) indicated that the distribution of a species can be explained by a trade-off between benefits met in a certain habitat and costs deriving from the exposure to risks. Dolphins, like all other animals, increase their benefits by performing behavioral strategies for staying where the likelihood of prey detection may be higher, and the risk of exposure may be lower.

A second hypothesis suggested that bufeos prefer meanders and confluences for being large size animals (dimensional reason). Meanders and confluences are sites where the river expands width, which makes these environments able to withstand a greater number of individuals compared to the main riverbed, that showed a width between 100 to 150 m, especially during the mating period, which coincides with the dry season. These meanders also have greater depths, which are preferred by the Asian (Braulik and Smith 2019; Baruah *et al.* 2012) and South American river dolphins (Martin and da Silva 2004b; Aliaga Rossel *et al.* 2006; Gómez-Salazar *et al.* 2012a).

The higher probability of encounters with bufeos in meanders may also be due to the sandbars, shallow and with a soft substrate. These characteristics might facilitate the detection and capture of small preys and provide calm mating areas (McGuire and Winemiller 1998; Trujillo 2000; Aliaga-Rossel and McGuire 2010).

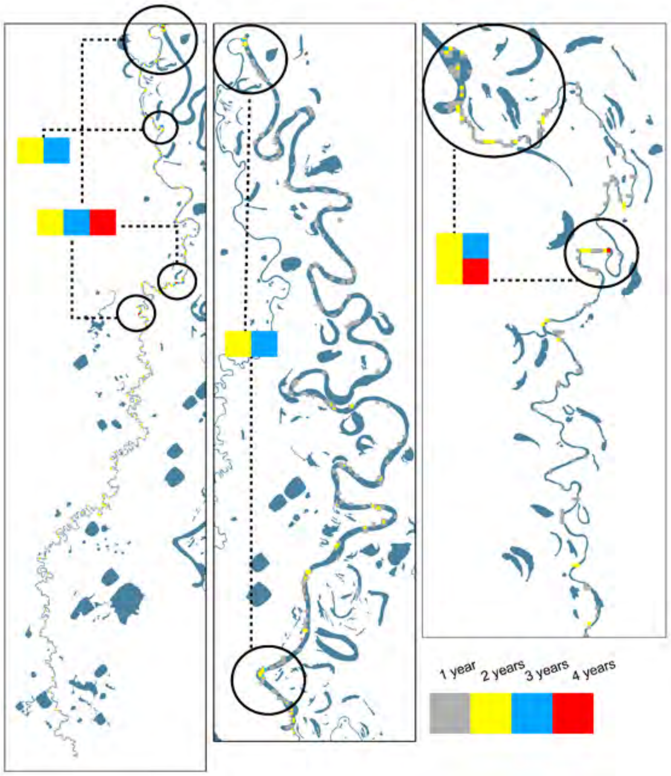

Figure 3. Accumulative occurrence maps showing sites with annual encounter repetitions. Black circles detail the meanders with more than a year of registers. The three sets of models are not drawn to scale.

The preference for habitats described here had been suggested and reported in several publications, but in all cases representing a single survey or a short period of time (McGuire and Winemiller 1998; Aliaga-Rossel 2002; Martin and da Silva. 2004a, b; Martin *et al.* 2004; Aliaga Rossel *et al.* 2006; McGuire and Henningsen 2007; Gómez-Salazar *et al.* 2012b; Guizada and Aliaga-Rossel 2016). However, this paper is the first to perform a multitemporal analysis based on that apparent preference, showing even the absence of historical records in certain areas. There were sites in Ibare River without records over all the sampled years (density of points null). These values influence the density of the points, reducing the probability of detecting bufeos to less than 80 %, even though some are meander sites. The same trend was observed for the Tijamuchi River, where the closer to the headwaters the lower the density of points, modifying the probabilities of sightings to fall with respect to the middle and lower parts of the river. In the Mamoré River, on the other hand, the distribution was more uniform.

The almost insignificant sighting record in Ibare River might be explained by the intensity of the anthropic pressure. This area records corresponded to the section between Puerto Almácen and Puerto Ballivian, area characterized for having high flow and boat traffic for different human activities (*e. g.*, tourism and subsistence fishing). Like with marine dolphins, the presence of the bufeos is probably constrained by disturbance factors such as boat traffic generating an effect of displacement (La Manna *et al.* 2013). Abdulla and Linden (2008) mention that boat traffic is recognized as one of the major causes of disturbance in aquatic ecosystems, and La Manna *et al.* (2014, 2016) state that characteristics such as frequency and duration strongly affect the amount of time dolphins spend at a site.

The distribution of cetaceans, on a large scale, can be influenced by five factors: 1) physicochemical, 2) climatological, 3) geomorphological, 4) biological, and 5) anthropogenic. However, some physicochemical variables (such as pH, conductivity, water transparency) seem not to influence the distribution of river dolphins, particularly *Inia boliviensis* (Guizada and Aliaga-Rossel 2016). In contrast, factors such as river bathymetry; differential, seasonal biomass; and mainly the intensity of human activities do influence on the presence of bufeos. For instance, estimating models that incorporate variables of these factors is the most appropriate way to explain and predict the distribution of river dolphins accurately. The identification of important habitat types such as confluences and meanders, which capacity to maintain populations of bufeos over time has been demonstrated, can be the most effective (and practical) way to determine important areas for their survival.

It is important to clarify that, for the Kernel density calculation, one of the parameters used for the estimation is the search radius. For this study, a search radius of 691 m was used to have an area of 1.5 km^2 due to dolphin movement. Martin and da Silva (2004a) showed, through satellite tracking, that the Amazon bufeo traveled between 20 to 100 km per day; some animals have even been seen for weeks using an area of 1 km^2. McGuire and Henningsen (2007), using photo ID, reported that the range of movement detected for the species in Bolivia is at least 60 km or 3 to 10 km daily. Therefore, the area used was similar to areas found in other regions.

As a conclusion, in three main rivers of the Mamoré River sub-basin, 345.8 km have been sampled with 30 surveys during a decade of observations. The 10-year database analyzed has allowed to monitor and to identify a clear preference by Bolivian bufeos for confluences and meander habitats in this river-complex in Bolivia.

The identification of these sites, which over time have hosted bufeos in higher concentrations of encounters, are mainly placed into protected areas such as Municipal Protected Area (APM) Ibare-Mamoré, and inside a territory of interest as a future protected area (Tijamuchi). Our data contribute with the main objective of conservation of this protected area and will promote the establishment of a new local Protected Area in the Beni region. We suggest this prompt action, considering that bufeos are a national and regional natural heritage.

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We dedicate this paper to the memory of Sydney Anderson. As a junior undergraduate EAR had the fortune of participating of a field trip with the Anderson-Yates expedition. Years later, EAR received a letter from Dr. Anderson – which made a world of difference in his career path -- encouraging him to follow his passion and interest to study bufeos. We also thank J. Salazar-Bravo for his invitation to contribute to this special issue. We thank the Whale and Dolphin Conservation (WDC), Rufford Foundation, and International Foundation for Science (IFS) for the support to Bolivian river dolphin conservation. Thanks to the field assistants in each survey, as well as our gratitude to our outboard motor divers. Special thanks to D. Salas Veizaga for the English review. Earlier versions of this manuscript were improved thanks to the insightful reviews by M. Marmontel (Mamirauá Institute for Sustainable Development, Tefé, Brazil) and an anonymous reviewer.

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Appendix 1

Script developed in the *writeRaster* function to create a bufeo occurrence probability per cell:

```
library(raster)
##Import the images by river per year
raster_river<-raster(‘nameRaster’)
##Graphing the raster
plot(raster_river)
##Summary of values per cell
summary(raster_river)
##A new empty raster is created that is the same size as the initial raster
newraster<-raster_river
newraster[] <- NA
getValues(raster_river)
newraster2<-getValues(raster_river)
## probability values of a normal distribution on the layer specifying the mean of the raster and its standard deviation
pnorm(newraster2, mean (newraster2), sd = #value SD raster_river)
values(newraster)<-pnorm(newraster2, mean(newraster2), sd = #value SD raster_river)
##Graph of the new raster
plot(newraster)
##Save the new raster with probability of occurrence values
writeRaster(newraster, file=’name’)
```

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Diet analysis of three rodent species sigmodontine in three cocoa production systems and forest in Alto Beni, Bolivia

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Alto Beni region in Bolivia, presents a mosaic of non-extensive family crops ranging from monocultures to agroforestry systems immersed in a matrix of secondary forest, while the primary forest remains on the steeper slopes. Very little is known about the biology of the rodent species that inhabit this area. Then, the objective of this work was to determine the diet and its variation among three species of sigmodontine rodents (*Akodon dayi, Euryoryomys nitidus* and *Oligoryzomys microtis*) from 11 agroforestry systems (SAF) of cacao (four traditional monoculture / simple SAF plots, three intermediate SAF and four complex SAF) and two secondary forests. We analyzed contents of the stomach, cecum and intestine for 41 *O. microtis* (simple-SAF *n* = 31, complex-SAF *n* = 4 and forest *n* = 6), for 11 *E. nitidus* (simple-SAF *n* = 6, intermediate-SAF *n* = 2, complex-SAF *n* =3 and forest *n* = 2) and for 10 *A. dayi* (simple-SAF *n* =5 and forest *n* =5). We calculated trophic niche width (Levin's Index) and measured the degree of niche overlap (an estimate of competition), using Pianka's Symmetric Overlaying Index. Significant differences in the diet specialization among species across habitats, were tested using the non-parametric Kruskal-Wallis test. A total of 55 food items were obtained and grouped into nine food categories: dicotyledonous vegetative structures, monocotyledonous vegetative structures, vascular tissue, spikelet, seeds, mycorrhizae, adult arthropods, larval arthropods, and others. The study species feed primarily on plants of the family Poaceae. No significant differences were found in the diet between species or between SAF and the forest ($P > 0.05$); in addition, there was no evidence of a noticeable overlay of trophic niches by habit type. In the studied season, we found that: *O. microtis* and *E. nitidus* are herbivorous omnivore; "generalist" simple-monoculture-SAF and "less generalist" in complex-SAF; besides, *O. microtis* is "generalist" in forest and *E. nitidus* is "specialist" in complex-SAF and in forest; while, *A. dayi* is herbivore-insectivore; "generalist" in simple-monoculture-SAF and in forest. Our results indicate that there is a strong relationship between, the type of plot where they were found and food availability in each habitat.

La región de Alto Beni en Bolivia presenta un mosaico de cultivos familiares no extensivos que van desde monocultivos hasta sistemas agroforestales en una matriz de bosque secundario, donde el bosque primario se mantiene en las laderas más pronunciadas. Poco se conoce de la biología de los roderos que habitan esta zona; así, el objetivo de este trabajo fue determinar la dieta y su variación entre tres especies de roedores sigmodontinos (*Akodon dayi*, *Euryoryzomys nitidus* y *Oligoryzomys microtis*) procedentes de 11 sistemas agroforestales (SAF) de cacao (cuatro parcelas monocultivo tradicional/SAF-simple, tres SAF-intermedio y cuatro SAF-complejo) y dos bosques secundarios. Analizamos los contenidos en estómago, ciego e intestino de 41 *O. microtis* (31 en SAF-simple, cuarto en SAF-complejo y seis en bosque), once de *E. nitidus* (seis en SAF-simple, dos en SAF-intermedio, tres en SAF-complejo y dos en bosque) y diez de *A. dayi* (cinco en SAF-simple y cinco en bosque). Calculamos frecuencia, diversidad e importancia relativa de la dieta; así como, la amplitud de nicho y estimamos el grado de competencia, (índice de Sobreposición Simétrico de Pianka). Las diferencias en la dieta (entre especies y hábitats), se calculó con la prueba de Kruskal-Wallis; y se estimó el grado de especialización en la dieta. Obtuvimos 55 ítems agrupados en nueve categorías alimenticias: restos vegetales dicotiledóneas, restos vegetales monocotiledóneas, tejido vascular, espiguillas, semillas, micorrizas, artrópodos adultos, artrópodos larvas, y otros. El principal recurso alimenticio para las tres especies fueron plantas de la familia Poaceae, y la dieta no varía significativamente entre especies ni entre SAF y bosque ($P > 0.05$). Tampoco existe marcada sobreposición de nichos tróficos por tipo de hábitats. Para la época de estudio, hallamos que *O. microtis* y *E. nitidus* son herbívoro-omnívoros; "generalistas" en SAF-simple-monocultivo, y "menos generalista" en SAF-complejo; además *O. microtis* es "generalista" en bosque y *E. nitidus*, es "especialista" en SAF-intermedio y bosque; mientras que *A. dayi* es herbívoro-insectívoro; "generalista" en SAF-simple-monocultivo y en bosque. De esta manera, existe una relación entre la dieta de los roedores en relación con el tipo de parcela donde se encuentran y con la disponibilidad de alimento en cada hábitat.

Keywords: Agroforestry system; diet; diet amplitude; microhistology; rodents; *Theobroma cacao*.

Introducción

La selección del alimento es una de las dimensiones más importantes del nicho ecológico de las especies, por lo cual la información sobre la dieta de los animales es un requisito para la mayoría de las investigaciones ecológicas (Vázquez1997; López-Cortés *et al.* 2007). Los roedores sigmodontinos muestran una amplia variedad de hábitos alimentarios, desde especies herbívoras hasta grados variables de omnivoría. Es posible encontrar especies frugívoras, granívoras, fungívoras y folívoras (Veloso y Bozinovic 2000; Polop *et al.* 2015). Sin embargo, Guabloche *et al.* (2002) indican que el régimen alimenticio de un roedor pequeño puede ser más variado y complejo que las categorías tróficas estándar (herbívoro o insectívoro).

En Sudamérica se han realizado estudios sobre la dieta de algunas especies de roedores sigmodontinos (Patton *et al.* 2015); sin embargo, estos reportes son escasos y dispersos. Además, es común que estudios locales de dieta se extrapolen y generalicen a través de la distribución geográfica de estas especies. Por lo tanto, estos resultados no necesariamente reflejan la variación presente en la dieta de las especies, debido a la alta heterogeneidad ambiental presente a lo largo de su distribución (Veloso y Bozinovic 2000; Cervantes 2014; Polop *et al.* 2015).

En Bolivia, si bien la riqueza de especies de roedores es bastante amplia (Aguirre *et al.* 2019), y se tiene una buena información sobre sus patrones de distribución (Anderson 1997; Patton *et al.* 2015), no existen información detallada sobre la biología, ecología y comportamiento de estos taxones. Por lo tanto, pocos estudios han abordado la dieta de los roedores sigmodontinos, siendo el de Osco (2000) uno de los pocos estudios en donde se ha estudiado este componente en diferentes ambientes. La mayoría de los reportes son registros ocasionales de los contenidos estomacales de roedores colectados en diferentes regiones (Mercado 1991; Anderson 1997) o información generada en otros países (Vázquez *et al.* 2000; Suarez y Bonaventura 2001; Silva 2005; Solari 2007).

Las variaciones de la dieta pueden deberse a cambios periódicos en los factores abióticos que generan cambios en la disponibilidad temporal de recursos (Krebs 1985). La mayoría de las especies de roedores tienen comportamientos de forrajeo flexibles que permiten respuestas adaptativas a contingencias ambientales (Vázquez 1997; Vázquez *et al.* 2000). La forma en que los animales responden a las contingencias incluye modificaciones en sus tiempos de alimentación, distribución de su actividad y tácticas de alimentación (Brown 2000). Para los roedores, cuya dieta puede ser muy diversa, esto puede jugar un papel importante en la depredación/dispersión de semillas (Traveset 1998; Xiao *et al.* 2006); pero también en la depredación postdispersiva de semillas y hongos, lo cual es considerado uno de los factores principales en la regeneración natural (Pons y Pausas 2007; Campos *et al.* 2007). Por otro lado, algunas especies de roedores son consideradas como plagas agrícolas (Tzab-Hernández y Macswiney 2014; De la Cruz y Sánchez-Soto 2016), aunque la mayoría están especializadas en el consumo de otros ítems, tales como los artrópodos, lo cual es benéfico para la agricultura (Aubry *et al.* 2003; Monge 2007; Montero y Gonzáles 2017). Por otro lado, también existen especies de roedores que pueden transmitir enfermedades y son consideradas zoonóticas por el hombre (Spotorno *et al.* 2000; Dobson y Foufopoulos 2001). Por lo tanto, es importante conocer no solo la riqueza y abundancia de roedores en diferentes zonas, sino también su dieta, para generar adecuados procesos de control, en caso de ser determinadas como efectivas plagas agrícolas o de alerta de zoonótica.

En la región de Alto Beni, al norte del departamento de La Paz, Bolivia, las actividades antropogénicas se han incrementado en las últimas décadas. La producción de cacao en fincas familiares se incentivó a partir de 1977 (July-Martinez 2007; Bazoberry y Salazar 2008), fragmentando y destruyendo el hábitat natural de muchas especies de vertebrados (Killeen *et al.* 2005; Killeen *et al.* 2007). Actualmente, el área tiene una intensa actividad productiva de cacao (*Theobroma cacao*) orgánico, donde se encuentran diferentes sistemas productivos que van desde monocultivos tradicionales (sistemas agroforestales simples) hasta sistemas agroforestales (SAFs) mucho más complejos (intermedio, complejo o sucesional) (Peñafiel 2000; CATIE 2002; Somarriba y Trujillo 2005; Milz 2010; Blum 2011). Dependiendo del tipo de manejo, estos sistemas presentan distintas especies leñosas de árboles y arbustos para proporcionar sombra al cacao y cítricos (*Citrus* sp.), obtener forraje y hojarasca como cobertura y abono orgánico (mantillo) (Villegas y Astorga 2005). Entonces, los recursos alimenticios y de refugio variarán según el tipo de sistema productivo, generando que los roedores respondan con cambios en su forrajeo, variando la selección de su dieta.

Akodon dayi es una especie monotípica y endémica para Bolivia (Anderson 1997; Pardiñas *et al.* 2015). Es conocida como rata de pasto diurna y es de hábitos terrestres (Anderson y Tarifa 1996; Emmons y Feer 1997). Si bien es considerada una especie común, encontrándosela en tierras bajas (250 msnm) hasta elevaciones intermedias (hasta 2,450 msnm; Myers *et al.* 1990), no se tienen mayores datos sobre su biología (Anderson 1997; Eisenberg y Redford 1999; Pardiñas *et al.* 2015). *Euryoryzomys nitidus* es conocida como rata de arroz (Percequillo 2015). Se encuentra en el oeste de Brasil y en el este de Perú y Bolivia (50 a 1.985 msnm). En Bolivia se encuentra en la selva tropical de las tierras bajas de las estribaciones andinas (Anderson 1997; Musser *et al.* 1998). Para Bolivia no hay datos detallados disponibles sobre hábitat, hábitos, comportamiento o alimentación (Anderson 1997; Patton *et al.* 2000; Percequillo 2015). *Oligoryzomys microtis* es conocida como rata pigmea del arroz, y tiene una amplia distribución que va desde el noroeste de Brasil, sur del río Amazonas hasta tierras bajas de Perú y Bolivia (Musser y Carleton 2005; Weksler y Bonvicino 2015). Es una especie de hábitos terrestres, común en gran parte de su amplia distribución. Debido a su capacidad de adaptarse a ambientes con cierto grado de degradación, puede llegar a ser considerada plaga agrícola (Eisenberg y Redford 1999; Patton *et al.* 2000). Se la considera una especie principalmente granívora, frugívora e insectívora.

De acuerdo con la hipótesis del disturbio intermedio (Connell 1978) es posible que en nuestro sistema de estudio exista una mayor riqueza de especies de roedores en los SAFs intermedios/complejos de cacao en comparación con los SAF simples con manejo orgánico como consecuencia de los distintos regímenes de perturbación. Es de esperar también que la dieta de los roedores será más selectiva y con una menor amplitud de nicho trófico en los SAFs intermedios/complejos debido a una mayor competencia entre las especies, mientras que en los SAF simples, estos roedores tendrán dietas más generalistas y con mayor amplitud de nicho trófico. El objetivo de este estudio fue analizar la dieta de tres especies de roedores sigmodontinos (*Akodon dayi*, *Euryoryzomys nitidus* y *Oligoryzomys microtis*) que habitan en diferentes tipos de sistemas de producción de cacao (*Theobroma cacao*) y bosque secundario circundante y determinar sí existe variación en la misma en función del tipo de sistemas de producción de cacao y bosque en el que se encuentran.

Material y Métodos

Área de estudio. El presente estudio se realizó en la región de Alto Beni, ubicado al noreste del departamento de La Paz a una distancia de 270 km de la ciudad. Su extensión es de 250,000 ha (15.182° S y 66.927° W), de las cuales el 50 % corresponden a bosque primario con tendencia descendente (Navarro y Maldonado 2002; Navarro 2011). Su altitud oscila entre 350 y 1500 msnm la temperatura media anual mínima es de 11 °C y la máxima es de 35 °C con una temperatura promedio anual de 26 °C; el área presenta una humedad relativa promedio anual de 70 y 80 % (Vega 2005; Ortiz -Gonzáles 2006). En zonas bajas (Covendo, 15.792° S y 66.977° W) la precipitación es de hasta 2000 mm. (Somarriba y Trujillo 2005; Blum 2011). La región de Alto Beni se caracteriza por una producción agrícola familiar intensiva. Los cultivos de mayor importancia económica son: arroz (*Oryza sativa*), banano (*Musa sp)*, cacao (*Theobroma cacao*), café (*Coffea arabica*), copuazu (*Theobroma grandiflora*), coco (*Cocos nucifera*) entre otros (Peñafiel 2000; Blum 2011). Las parcelas familiares se distribuyen en la zona formando una franja de cultivos comerciales destinados para la exportación (CATIE 2002; Somarriba y Trujillo 2005; Blum 2011). La zona de estudio es un valle que se extiende por ambos márgenes del río Alto Beni, a cuyos márgenes corre la carretera desde la localidad de Sapecho hacia Covendo (de este a oeste) y de Palos Blancos que presenta bosque de pie de monte que reúne elementos de flora y fauna de la parte alta (bosque montano húmedo) y de las tierras bajas y amazónicas, por lo que la riqueza de especies es muy alta en comparación con otras regiones del país.

Trabajo de campo. El presente trabajo se realizó en el marco del proyecto "Investigación sobre funciones ecosistémicas en sistemas de producción de cacao en Alto Beni". Se establecieron 15 parcelas de muestreo con la finalidad de mantener el muestreo lo más balanceado posible. Sin embargo, en dos de ellas no se colectó ningún roedor. Por lo que se trabajó en 13 parcelas, 11 con diferente tipo de producción de cacao y dos bosques intervenidos ubicadas a lo largo de la carretera entre Palos Blancos y Covendo. Las parcelas estuvieron separadas al menos 500 m entre ellas con la finalidad de mantener la independencia de los datos. De las 11 parcelas, cuatro fueron agroforestales simples o monocultivos (sistema con manejo orgánico, sombra temporal con cobertura de leguminosas, aplicación de compost y abono orgánico), tres agroforestales intermedios (sistema con manejo orgánico, sombra regular donde existe entre dos y diez especies vegetales asociadas: leguminosas, frutales y maderables), cuatro agroforestales complejos o sucesiones (sistema que trata de imitar un ecosistema natural de bosque, más de diez especies frutales, maderables asociadas y de regeneración natural) y dos bosques con poca intervención (bosque secundario con baja perturbación humana con sucesión natural de especies y ningún tipo de manejo; Figura 1). El muestreo fue realizado entre agosto a septiembre y noviembre a diciembre del 2015.

En cada parcela se estableció un cuadrante de $200 m^2$ por sitio y se estableció una grilla de diez por diez estaciones de trampeo separadas por 10 metros entre sí, en cada parcela se colocó un total de 100 estaciones de muestreo, con 100 trampas Sherman. Las trampas fueron cebadas con una mezcla de hojuelas de avena y atún embebidos en esencia de vainilla para formar una pasta (Tarifa y Yesen 2001). El muestreo se realizó durante tres noches consecutivas en cada sitio y las trampas fueron revisadas cada mañana, siendo reemplazadas por trampas limpias cuando tenían capturas (Poleo *et al.* 2006).

Todos los especímenes capturados fueron recolectados siguiendo las directrices de la Sociedad Americana de Mastozoología (Sikes *et al.* 2016). El tracto digestivo de cada

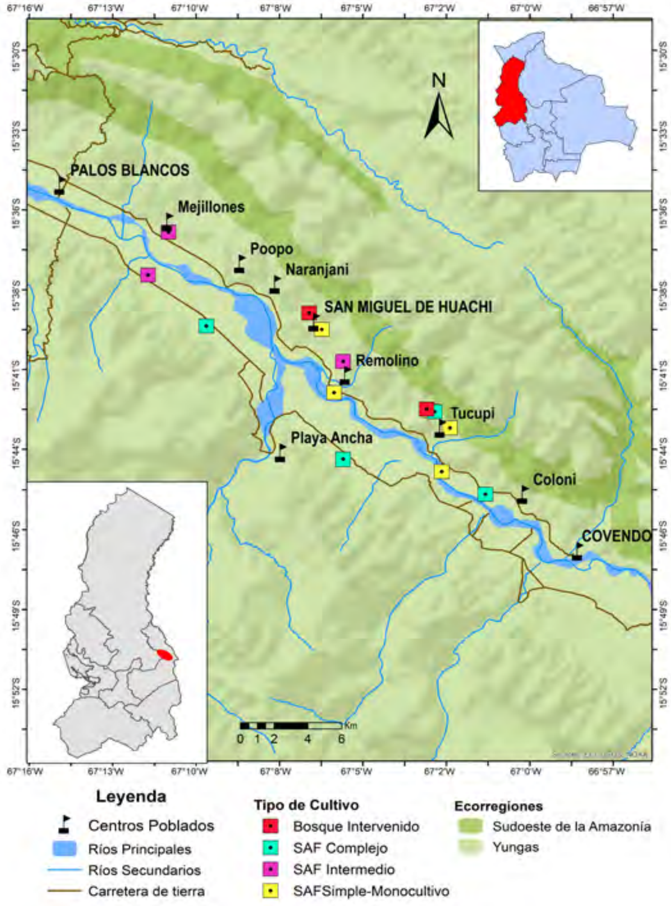

Figura 1. Mapa de la zona de estudio en el cual se indican las tres condiciones de los Sistemas Agroforestales (SAF) y bosque intervenido muestreados en este trabajo.

individuo colectado se procesó *in situ* fijándolo en alcohol al 70 %. Los ejemplares fueron preservados en alcohol al 96 % para su posterior identificación. De cada uno de los sitios de muestreo se elaboró un catálogo de referencia de especies vegetales menores a 1.5 m de alto presentes en el lugar, a fin de poder utilizarlo al momento de obtener los ítems alimenticios y contar con la información sobre la disponibilidad y diversidad de los recursos alimentarios de cada parcela.

Trabajo del laboratorio. De cada espécimen se analizaron los contenidos del estómago, ciego e intestino (grueso-delgado; Osco 2000). Cada contenido se disgregó, homogenizó y filtró (Meserve 1981; Noblecilla y Pacheco 2012). Posteriormente fue separado en dos fracciones: partículas pequeñas (< 0.7 mm) y partículas grandes (> 0.7 mm; Guabloche *et al.* 2002). Cada fracción fue examinada usando un estereomicroscopio a un aumento de 45X. Las partículas grandes fueron separadas y almacenadas en viales Eppendorf (1.5 ml) para su identificación y montaje en gelatina glicerada. Las partículas pequeñas se distribuyeron homogéneamente sobre portaobjetos y se dejaron secar. Para la cuantificación de categorías alimenticias se rehidrató cada placa con una gota de alcohol al 70 %, se cubrió con un cubre objetos y se cuantifico usando un microscopio óptico a 40 X ó 100 X aumentos (Cortés *et al.* 2002). Cada placa contuvo 20 campos de los cuales diez fueron evaluados (Holechek y Vavra 1981; Holechek *et al.*1982). Para cada uno de los órganos se realizaron tres placas y se observaron 30 campos por sector, tomando en total 90 campos por cada roedor.

Análisis de los datos. La composición de la dieta fue determinada por comparación directa con el catálogo de referencia elaborado con plantas colectadas del área de estudio (Apéndice 1). Para el análisis de los ítems alimenticios encontrados se calculó la frecuencia de presencia (Fn %) para cada categoría en cada sector del tracto digestivo, de acuerdo con la siguiente fórmula: Fn (%) =[N° de campos donde la categoría alimenticia esta presente/ N° total de campos examinados] x 100.

Para determinar la dieta de las especies de roedores en los diferentes SAFs y el bosque, los ítems alimenticios obtenidos se agruparon de acuerdo a su categoría taxonómica y tipo de recurso en restos de estructuras vegetativas dicotiledóneas y monocotiledóneas (tallos-hojas), tejido vascular (morfotipos), espiguillas (enteras y partes), semillas, micorrizas (esporocarpos-hifas), artrópodos adultos, artrópodos larvas, y otros. Para la comparación de la dieta a nivel de especies y entre tipos de hábitats se emplearon los promedios de la agrupación de cada categoría taxonómica y tipo de recurso. Para este análisis se utilizó una prueba no paramétrica de Kruskal-Wallis en el programa SPSS Statistics vers.23 (IBM Corporation. Somer, NewYork).

Para describir la diversidad en la dieta de cada especie de roedor se utilizaron datos de frecuencia de cada ítem al interior de cada categoría. Las curvas de rango-abundancia se elaboraron examinando la abundancia de dichos ítems por tipo de hábitat. Se estimó la importancia Orden/familia de los ítems vegetales o de artrópodos consumidos por las tres especies de roedores en los cuatro hábitats. Para ello se utilizaron datos de frecuencia de ocurrencia absoluta de cada ítem y se aplicó el índice de valor de importancia de los recursos (IVIR = ∑ (*PXi*), modificado por Amaya 1991). Este índice ha sido utilizado en análisis de la dieta de mamíferos menores (Maguiña 2011). Donde *PXi* es la frecuencia de uso del recurso *i* por parte de la especie *X* de roedor (frecuencia total de recursos utilizados por la especie *X* de roedor). El recurso para este estudio se refiere al ítem en particular.

Para determinar el nivel de variación de uso del recurso (*ítem en particular*) en la dieta de cada especie, se calculó la amplitud de nicho con el Índice de Levins (Levins 1968): *B* = 1 / ∑ *Pi*2. Donde *B* es la medida de amplitud de nicho trófico y *Pi* es la proporción del recurso encontrado en cada unidad de evaluación.

Posteriormente, se aplicó la ecuación de Levins estandarizada, donde valores cercanos a 0 indican que la especie es más especialista, y valores cercanos a 1 indican que es una especie generalista: *Ba* = (*B* - 1) / (*n* - 1); donde *Ba* es la amplitud de nicho estandarizada, *B* es la medida de amplitud de nicho y *n* es el número de categorías alimentarias (ítems) consumidos por la especie.

El grado de competencia por el uso de recursos alimenticios (ítems) se calculó con el índice de sobreposición simétrico de Pianka (Pianka 1973) y el índice modificado de Morisita (Horn 1966). El Índice de Sobreposición se considera alto para valores sobre 0.75 y bajo para menores a 0.50 (Noblecilla-Huiman 2008).

Se calculó la media general de cada categoría consumida (la mayor frecuencia de una categoría consumida, Dytham 2001). Posteriormente se determinó el coeficiente de variación (CV) a partir de las medias y desviaciones estándar de cada categoría. El grado de especialización en la dieta se determinó utilizando el coeficiente de variación (CV) para cada categoría alimenticia de cada especie con nueve o más individuos. En este análisis no se tomó en cuenta la condición del hábitat. Se consideraron valores de CV menores a 30 % como indicativos de alguna preferencia para las categorías alimenticias (Solari 2007; Noblecilla-Huiman 2008; Cervantes 2014).

Resultados

En todas las parcelas de trabajo se capturaron 13 especies de roedores, de las cuales solamente *Oligoryzomys microtis, Euryoryzomys nitidus* y *Akodon dayi* contaron con el suficiente número de individuos para poder hacer el estudio. Del resto de las especies (*Microryzomys minutus*, *Hylaeamys perenensis*, *Hylaeamys megacephalus*, *Neacomys vargasllosai*, *Oecomys bicolor* y *Rhipidomys nitela, Proechimys brevicauda* y *Proechimys* sp.) se colectaron menos de cinco especímenes por especie. Se analizó la dieta de 64 roedores: 41 de *O. microtis* (*n* = 31 en SAF simple, *n* = 4 en SAF complejo y *n* = 6 en bosque), 13 de *E. nitidus* (*n* = 6 en SAF simple, *n* = 2 en SAF intermedio, *n* = 3 en SAF complejo y *n* = 2 en bosque) y 10 de *A. dayi* (*n* = 5 en SAF simple y *n* = 5 en bosque), registrándose un total de 55 ítems alimenticios (Apéndice 2).

Oligoryzomys microtis. Esta especie consumió principalmente ítems de la categoría restos vegetales en todos los sitios donde fue colectada (Tabla 1). En SAF simple se encontró un total de 35 ítems y una baja pendiente en su gráfica de rango-abundancia indicando una mayor equitatividad de los ítems alimenticios (Figura 2). La categoría de restos vegetales monocotiledóneas fue la más abundante (33.62 %), seguido de micorrizas (23.29 %) y restos vegetales dicotiledóneas (21.25 %; Tabla 1). Dentro de la categoría micorrizas el ítem más dominante fueron las hifas intraradicales de *Glomus macrocarpum* (6.70 %), respecto a los restos vegetales, la hoja de la morfoespecie *Bomarea* sp. (5.27 %) fue la más consumida, seguida de los tallos de *Paspalum conjugatum* (4.16 %) y *Paspalum paniculatum* (4.44 %) (plantas monocotiledóneas). En menor porcentaje se registraron tallos de *Hydrocotyle* sp. (4.73 %) y de *Acalypha stricta* (3.08 %; plantas dicotiledóneas). Entre los artrópodos adultos, el orden Hymenoptera (2.08 %) fue el más consumido, seguido de la familia Formicidae (1.18 %) y el orden Hemiptera en menor frecuencia (0.97 %; Figura 2). En SAF complejo, los 12 ítems consumidos presentan una curva de rango-abundancia con mayor pendiente y menor equitatividad que para SAF simple. La categoría más abundante fue restos vegetales monocotiledóneas (81.11 %), seguido de la categoría otros (14.45 %) y restos vegetales dicotiledóneas (4.44 %). En esta última, los tallos de *Axonopus compressus* (21.11 %), *Imperata* sp. (18.61 %) y *Oplismenus hirtellus* (16.67 %; monocotiledóneas) fueron los más frecuentes (Figura 2). En las parcelas de bosque también se registraron 12 ítems y una curva similar a SAF complejo (Figura 2). Se registró un mayor porcentaje de restos vegetales dicotiledóneas (28.33 %), seguido de restos vegetales monocotiledóneas (27.78 %), espiguillas (22.78 %) y la categoría otros (21.11 %), donde los tallos de *Paspalum paniculatum* (20.00 %; monocotiledónea) e *Ipomoea* sp. (11.67 %; dicotiledónea) fueron los ítems más frecuentes. *O. microtis* fue la única especie que presentó restos de alga Chlorophyta (4.44 %) en su dieta. El análisis de la amplitud de nicho indica que *O. microtis* tiene una dieta amplia o generalista en parcelas SAF simple-monocultivo, catalogándolo como omnívoro. En SAF complejo es herbívoro, ya que consume principalmente restos vegetales presentando una dieta menos amplia por ser más especialista. En bosque, es omnívora, de dieta amplia y más generalista, que en SAF complejo (Tabla 2).

Euryoryzomys nitidus. Esta especie presentó una dieta más omnívora, donde las categorias mas importantes variaron según el tipo de sistema de producción (Tabla 1). El SAF simple presentó mayor número de ítems alimenticios en su dieta, con 20 en total y una curva de rango-abundancia con una pendiente moderada (Figura 3). La categoría artrópodos adultos (26.66 %) fue la más abundante, seguida de la categoría otros (24.07 %) y espiguillas (22.41 %). Las categorías restos vegetales monocotiledóneas (10.75 %), dicotiledóneas (7.78 %), artrópodos larvas (7.22 %) y tejido vascular (morfotipos; 1.11 %) fueron menos abundantes. Para los artrópodos adultos, el ítem Coleóptera (22.96 %) fue el más dominante, aunque también se registraron larvas de Hymenoptera (7.22%) en este sistema de producción. En el SAF intermedio, se registraron 12 ítems alimenticios distribuidos de manera más equitativa. La categoría restos vegetales monocotiledóneas fue la más abundante (32.23 %) seguida de la categoría otros (31.67 %) y restos vegetales dicotiledóneas (18.34 %), donde los ítems tallos de *Cyperus chalaranthus* (15.56 %; monocotiledónea) e *Iresine diffusa* (10.56 %; dicotiledónea) y hojas de *Anthurium* sp. (8.89 %; monocotiledónea) fueron los más frecuentes. No se reportó consumo de artrópodos ni micorrizas en este tipo de sistema, pero sí ítems de las categorías espiguilla: *Paspalum paniculatum* (12.20 %; monocotiledónea) y semillas: *Polygonum* sp. (5.56 %; dicotiledónea). El SAF complejo también presentó 12 ítems alimenticos presentando una curva de rango abundancia

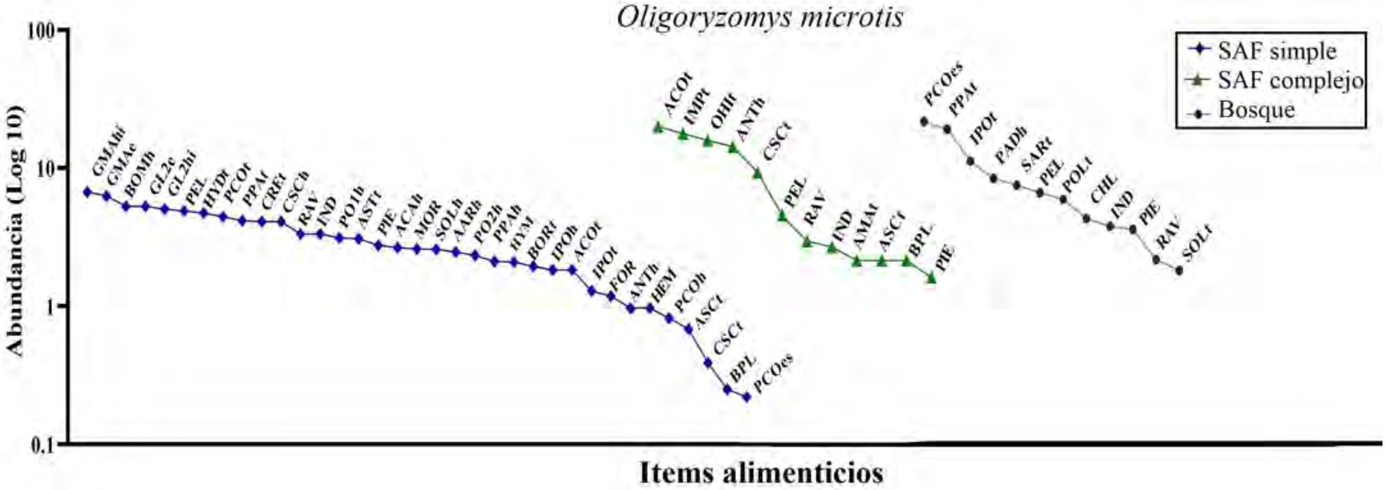

Figura 2. Curvas de rango-abundancia para las especies de ítems consumidos por *Oligoryzomys microtis* en SAF simple, SAF complejo y el bosque. Orden de la muestra desde la especie de ítem más abundante hasta la menos abundante. SAF simple = Sistema agroforestal simple-monocultivo; SAF intermedio = Sistema agroforestal intermedio; SAF complejo = Sistema agroforestal complejo; Bosque = Bosque secundario. a = arista, e = esporocarpos, es = espiguilla, g = gluma, h = hoja, hi = hifas intraradicales, l = lemma, p = pálea, s = semilla, t = tallo, ACA= *Acalypha* sp., AAR= *Acalypha arvensis*, AMA = *Amaranthaceae* sp., ANT = *Anthurium* sp., ASC = *Asclepiadaceae* sp., AST = *Acalypha stricta* , ACO = *Axonopus compressus*, BOM = *Bomarea* sp., BPL = bolsa plástica, BOR = *Borreria* sp., CRE = *Callisia repens*, CSC = *Costus scaber*, CHL = Chlorophyta, GMA = *Glomus macrocarpum*, GL2 = *Glomus* sp2., HYD = *Hydrocotyle* sp., HYM = Hymenoptera, IMP = *Imperata* sp., IPO = *Ipomoea* sp., IND = indeterminado, MOR = morfotipo, OHI = *Oplismenus hirtellus*, PCO = *Paspalum conjugatum*, PPA = *Paspalum paniculatum*, PEL = pelos, PIE = piedras, PAD = *Piper aduncum*, PO1 = *Poaceae* sp1., PO2 = *Poaceae* sp2., POL = *Polygonum* sp., RAV = restos de avena, SOL = *Solanum* sp., SAR = *Sorghum arundinaceum*.

Tabla 1. Composición de la dieta, agrupada en categorías, de *Akodon dayi*, *Euryoryzomys nitidus* y *Oligoryzomys microtis* en los diferentes sistemas de producción de cacao para la época de transición húmeda-seca. Se muestra la ocurrencia de individuos y sus porcentajes (entre paréntesis) en cada sitio de muestreo.

	SAF simple	**Bosque**	**SAF simple**	**SAF inter**	**SAF complejo**	**Bosque**	**SAF simple**	**SAF Complejo**	**Bosque**
		Akodon dayi			***Euryoryzomys nitidus***			***Oligoryzomys microtis***	
Categoría	*n* = 5	*n* = 5	*n* = 6	*n* = 2	*n* = 3	*n* = 2	*n* = 31	*n* = 4	*n* = 6
Restos vegetales dicotiledóneas	41 (9.11 %)	37 (8.22 %)	42 (7.78 %)	30 (18.34 %)	4 (1.48 %)	102 (56.65 %)	593 (21.25 %)	16 (4.44 %)	153 (28.33 %)
Restos vegetales monocotiledóneas	63 (14.00 %)	68 (15.11 %)	58 (10.75%)	58 (32.23 %)	20 (7.40 %)	31 (17.25 %)	938 (33.62 %)	292 (81.11 %)	150 (27.78 %)
Semillas				6 (5.56 %)	4 (1.48 %)				
Espiguillas	96 (21.34 %)	17 (3.77 %)	121 (22.41 %)	22 (12.20 %)			6 (0.22 %)		123 (22.78 %)
Micorrizas	32 (7.11 %)	124 (27.56 %)			96 (35.56 %)		650 (23.29 %)		
Artrópodos Adultos	170 (37.78 %)	130 (28.89 %)	144 (26.66 %)		95 (35.18 %)		118 (4.23 %)		
Artrópodos larvas			39 (7.22 %)						
Tejido vascular (Morfotipos)	22 (4.89 %)	37 (8.23 %)	6 (1.11 %)		7 (2.59 %)		79 (2.59 %)		
Otros	26 (5.77 %)	37 (8.22 %)	130 (24.07 %)	57 (31.67 %)	44 (16.31 %)	47 (26.10 %)	406 (14.80 %)	52 (14.45 %)	114 (21.11 %)
Porcentaje total	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

SAF simple = Sistema agroforestal simple-monocultivo; SAF inter = Sistema agroforestal intermedio; SAF complejo = Sistema agroforestal complejo; Bosque = Bosque secundario.

con mayor pendiente que en los dos anteriores sistemas (Figura 3). Las categorías con mayor consumo fueron micorrizas (35.56 %), artrópodos adultos (35.18 %) y otros (16.31 %). Las categorías menos consumidas fueron restos vegetales monocotiledóneas (7.40 %), tejido vascular (morfotipos; 2.59 %), restos vegetales dicotiledóneas (1.48 %) y semillas (1.48 %). En la categoría de micorrizas se encontraron en mayor frecuencia restos de esporocarpos de *Glomus clavisporum* (35.56 %); en la de artrópodos adultos, los ítems Coleóptera (21.48 %) e Hymenoptera (13.70 %) fueron los más frecuentes; mientras que, en restos vegetales, los restos de hoja de *Anthurium* sp. (4.44 %) y de tallo de *Cyperus chalaranthus* (2.96 %; monocotiledóneas) fueron las más frecuentes. El bosque presentó el menor número de ítems, con solo 10 y una pendiente pronunciada (Figura 3). En el bosque esta especie mostró una preferencia por restos vegetales dicotiledóneas (56.65 %) y la categoría otros (26.10 %), y en menor preferencia a los restos vegetales monocotiledóneas (17.25 %); el ítem hoja de *Desmodium* sp. (33.33 %; dicotiledónea) fue el más frecuente, pero también se hallaron restos de tallo de *Oplismenus hirtellus* (13.89 %) (monocotiledónea), el tallo *Acalypha stricta* (12.22 %) y la hoja de *Acalypha arvensis* (8.89 %) (dicotiledóneas). En estas parcelas tampoco se reportaron restos de artrópodos y micorrizas. El análisis de amplitud del nicho indica que *E. nitidus* en parcelas del SAF simple-monocultivo es un consumidor generalista y de dieta amplia, catalogándolo como omnívoro. En el SAF complejo es generalista y de dieta menos amplia comparada con SAF simple; mientras en parcelas SAF intermedio y bosque es herbívoro y

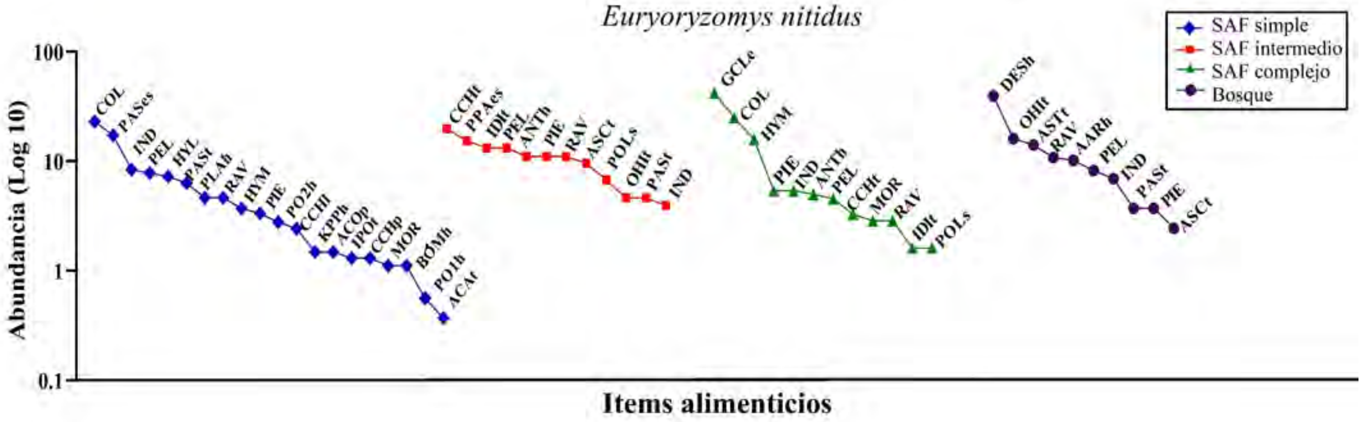

Figura 3. Curvas rango-abundancia para las especies de ítems consumidos por *Euryoryzomys nitidus* en SAF simple, SAF intermedio, SAF complejo y el bosque. Orden de la muestra desde la especie de ítem más abundante hasta la menos abundante. SAF simple = Sistema agroforestal simple-monocultivo; SAF intermedio = Sistema agroforestal intermedio; SAF complejo = Sistema agroforestal complejo; Bosque = Bosque secundario. a = arista, e = esporocarpos, es = espiguilla, g = gluma, h = hoja, hi = hifas intraradicales, l = lemma, p = pálea, s = semilla, t = tallo, ACA = *Acalypha* sp., AAR = *Acalypha arvensis*, ASC = *Asclepiadaceae* sp., AST = *Acalypha stricta*, ANT = *Anthurium* sp., ACO = *Axonopus compressus*, BOM = *Bomarea* sp., COL = Coleoptera, CCH = *Cyperus chalaranthus*, DES = *Desmodium* sp., GCL = *glomus clavisporum*, HYM = Hymenoptera, HYL = Larvas Hymenoptera, IPO = *Ipomoea* sp., IDI = *Iresine difusa*, IND = indeterminado, KPP = *Kudan pueraria phaseoloides*, MOR = morfotipo, OHI = *Oplismenus hirtellus*, PAS = *Paspalum* sp., PLA = *Plantago* sp., PPA = *Paspalum paniculatum*, PEL = pelos, PIE = piedras, PO1 = *Poaceae* sp1., PO2 = *Poaceae* sp2., POL = *Polygonum* sp., RAV = restos de avena.

Tabla 2. Valores del índice de Levins y Levins estandarizado para la dieta de tres especies de roedores sigmodontinos en diferentes sistemas de producción de cacao (*Theobroma cacao*), en Alto Beni (La Paz-Bolivia) durante el periodo de transición húmeda-seca.

Especie	Sitio	Índice de Levins *B*	Levins estandarizado *BA*
Oligoryzomys microtis	SAF simple	26.54	0.65
	SAF complejo	6.91	0.54
	Bosque	9.26	0.64
Euryoryzomys nitidus	SAF simple	10.47	0.73
	SAF inter	8.06	0.32
	SAF complejo	5.80	0.53
	Bosque	3.66	0.33
Akodon dayi	SAF simple	25.82	0.75
	Bosque	18.51	0.70

SAF simple = Sistema agroforestal simple-monocultivo; SAF inter = Sistema agroforestal intermedio; SAF complejo = Sistema agroforestal complejo; Bosque = Bosque secundario.

consumidor especialista, ya que consume principalmente restos vegetales (Tabla 2).

Akodon dayi. Esta especie consumió principalmente ítems de la categoría artrópodos adultos en todos los sitios donde fue colectada. Al igual que para las otras dos especies, también se encontró una mayor cantidad de ítems alimenticios en SAF simple, 28 en total (Figura 4), donde la pendiente de la curva de rango abundancia es muy poco pronunciada. La categoría más consumida fue artrópodos adultos (37.78 %); donde los ítems: restos de los órdenes Hymenoptera (13.56 %), Coleóptera (10.67 %) y Díptera (5.56 %) fueron los más consumidos. La categoría espiguillas (21.34 %) también fue muy consumida, donde el ítem *Paspalum paniculatum* (5.11 %) y *Paspalum conjugatum* (4.89 %) fueron las más frecuentes. Las categorías restos vegetales monocotiledóneas (14.00 %) y dicotiledóneas (9.11 %) fueron menos consumida, donde el ítem hoja de la morfoespecie *Hydrocotyle* sp. (5.78 %; dicotiledónea) fue la más frecuente. Para las parcelas de bosques se reportó un total de 20 ítems diferentes en la dieta de *A. dayi* y una pendiente poco pronunciada en la curva de rango-abundancia (Figura 3). Las categorías más consumidas fueron artrópodos adultos (28.89 %), micorrizas (27.56 %) y restos vegetales monocotiledóneas (15.11 %) y dicotiledóneas (8.22 %; Figura 4). Con relación a los ítems de artrópodos adultos, los *órdenes más frecuentes fueron* Hymenoptera, pero en específico la familia Formicidae (12.22 %), otros Hymenoptera (7.33 %) y Díptera (6.22 %). No se registraron restos de coleópteros. Los restos de esporocarpos de *Glomus fasciculatum* (10.22 %) y *Glomus* spp. (7.11 %), se reportan por primera vez en la dieta de esta especie. *Akodon dayi* se cataloga como generalista, de dieta amplia, según el análisis de amplitud de nicho; tanto en parcelas SAF simple-monocultivo, como en bosque intervenido (Tabla 2).

De acuerdo con los valores del IVIR las tres especies de roedores tienen como principal recurso en su dieta plantas de la familia Poaceae con 0.772 de IVIR en SAF simple-monocultivo; 0.233 de IVIR en SAF intermedio; 0.564 IVIR en SAF complejo y 0.754 de IVIR en bosque (Apéndice 3). En el SAF simple el orden de hongos Glomerales es la más importante para la especie *O. microtis*, el orden Coleóptera para *E. nitidus* y el orden Hymenoptera para *A. dayi*. En el bosque, el orden Glomerales es la más importante para *A. dayi*, mientras que para *E. nitidus* lo son las familias Papilionaceae y Euphorbiaceae. Por otro lado, los resultados del IVIR en SAF intermedio (tomando valores solo de *E. nitidus*) mostraron que el recurso principal es la familia Poaceae con 0.21 de IVIR. En el SAF complejo (sumando los valores de dos especies) mostraron como principal recurso a la familia Poaceae con 0.56 de IVIR. Sin embargo, el uso de los recursos varía entre las tres especies y entre los sitios estudiados (Tabla 3, Apéndice 3).

De manera general, en el SAF simple las tres especies de roedores consumen en mayor frecuencia restos vegetales. En el SAF intermedio la única especie presente, *E. nitidus,* tuvo restos vegetales como su categoría principal de

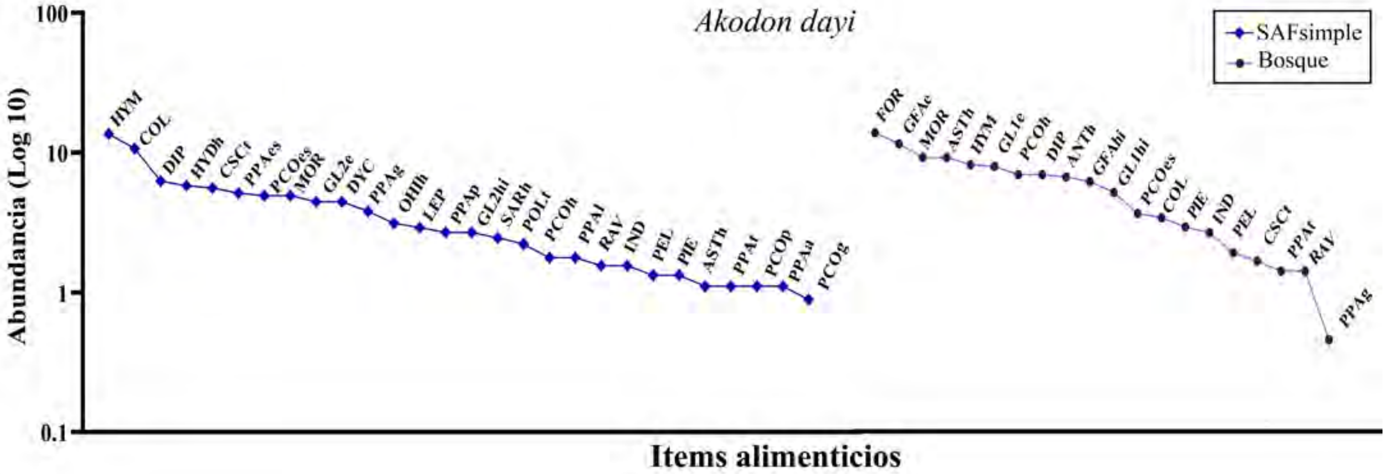

Figura 4. Curvas rango-abundancia para las especies de ítems consumidos por *Akodon dayi* en SAF simple y el bosque. Orden de la muestra desde la especie de ítem más abundante hasta la menos abundante. SAF simple = Sistema agroforestal simple-monocultivo; SAF intermedio = Sistema agroforestal intermedio; SAF complejo = Sistema agroforestal complejo; Bosque = Bosque secundario. a = arista, e = esporocarpos, es = espiguilla, g = gluma, h = hoja, hi = hifas intraradicales, l = lemma, p = pálea, s = semilla, t = tallo, ANT = *Anthurium* sp., AST = *Acalypha stricta* , CSC = *Costus scaber*, COL = Coleóptera, DIP = Díptera, DYC = Dyctioptera, FOR = Formicidae, GFA = *Glomus fasciculatum*, GL1 = *Glomus* sp1., GL2 = *Glomus* sp2., HYD = *Hydrocotyle* sp., HYM = Hymenoptera , IND = indeterminado, LEP = Lepidóptera, MOR = morfotipo, OHI = *Oplismenus hirtellus*, PCO = *Paspalum conjugatum*, PPA = *Paspalum paniculatum*, PEL = pelos, PIE = piedras, POL = *Polygonum* sp., RAV = restos de avena, SAR = *Sorghum arundinaceum*.

Tabla 3. Índice del valor de importancia de principales recursos de las especies consumidas por los roedores *Akodon dayi*, *Euryoryzomys nitidus* y *Oligoryzomys microtis*. Se muestra el uso de recurso (Pxi) y el índice de valor de importancia de recursos (IVIR) en cada sitio de muestreo, se marcan con * los valores mayores a 0.1 y los resultados de IVIR mayores a 0.1 se encuentran resaltados con negrillas.

Familia/Orden	Especie/Morfoespecie	SAF simple				SAF inter		SAF complejo			Bosque			
		O.mi	***E.ni***	***A.da***	***IVIR***	***E.ni***	***IVIR***	***O.mi***	***E.ni***	***IVIR***	***O.mi***	***E.ni***	***A.da***	***IVIR***
		Pxi	***Pxi***	***Pxi***		***Pxi***		***Pxi***	***Pxi***		***Pxi***	***Pxi***	***Pxi***	
Dicotyledoneae														
Convolvulaceae	*Ipomoea* sp.	0.03	0.01		0.04						0.12		0.13	***0.25***
Papilionaceae	*Desmodium* sp.											0.26*		***0.26***
Polygonaceae	*Polygonum* sp.			0.02	0.02	0.04	0.04		0.02	0.02	0.06	0.23*		***0.29***
Monocotyledoneae														
Araceae	*Anthurium* sp.	0.01			0.01	0.09	0.09	0.10	0.04	***0.19***			0.02	0.02
Cyperaceae	*Cyperus chalaranthus*		0.04		0.04	0.16*	***0.16***		0.03	0.03			0.05	0.06
Poaceae	*Axonopus compressus*	0.02	0.02		0.03			0.21*		***0.21***			0.11	0.11
	Imperata sp.							0.17*		***0.19***				
	Oplismenus hirtellus			0.03	0.03	0.04	0.04	0.17*		***0.17***		0.12	0.09	***0.20***
	Paspalum conjugatum	0.06		0.09	0.14						0.23*		0.04	***0.26***
	Paspalum paniculatum	0.06		0.16*	***0.22***	0.13	0.13				0.20*		0.01	***0.21***
	Paspalum sp.		0.23*		***0.24***	0.04	0.04					0.03		0.03
Glomeromycetes														
Glomerales	*Glomus clavisporum*								0.36*	***0.36***				
	Glomus sp2.	0.10*		0.07	***0.17***									
Insecta														
	Coleoptera sp1.			0.07	0.07									
Coleoptera	Coleoptera sp4.		0.23*		***0.23***									
	Coleoptera sp5.								0.22*	***0.22***				

SAF simple = Sistema agroforestal simple-monocultivo; SAF inter = Sistema agroforestal intermedio; SAF complejo = Sistema agroforestal complejo; Bosque = Bosque secundario. O.mi = *Oligoryzomys microtis*; E.ni = *Euryoryzomys nitidus*; A.da = *Akodon dayi*.

consumo. En el SAF complejo *O. microtis* presentó a los restos vegetales como su primordial categoría alimenticia y *E. nitidus* a la categoría micorrizas como su recurso principal. Finalmente, en el bosque las tres especies de roedores consumen primordialmente restos vegetales (tallos, hojas, espiguillas entre otros). A pesar de estas diferencias cualitativas en la dieta, las pruebas de Kruskal-Wallis concluyen que no hay diferencias significativas ni entre especies ($H = 2.213$, *g.l.* = 2, $P = 0.331$), ni por sitio de estudio ($H = 6.700$, *g.l* = 3, $P = 0.082$).

Las medidas de sobreposición de nicho trófico mostraron un rango con valores bajos (*ISP* = 0.11; *IMM* = 0.10) entre *E. nitidus* y *A. dayi*; y entre *E. nitidus* y *O. microtis* (ISP = 0.22; *IMM* = 0.21). Mientras que, al comparar *O. microtis* con *A. dayi* se tuvo el mismo valor de solapamiento con ambos índices (*ISP* = 0.26; *IMM* = 0.26). Estos valores representan baja sobreposición e indican poca similitud entre los ítems de las dietas de estas especies de roedores y sugieren que no hay competencia por alimento entre ellos.

El análisis del coeficiente de variación (CV) más bajo obtenido fue para *A. dayi* en la categoría restos vegetales monocotiledóneas con 5.4 % y dicotiledóneas 7.3 %. Para *E. nitidus* el CV más bajo fue para la categoría restos vegetales monocotiledóneas 46.2 %; y para *O. microtis* el CV más bajo fue también para la categoría restos vegetales monocotiledóneas, confirmando así la alta preferencia por estas categorías alimenticias (Tabla 4).

Discusión

La composición de la dieta mostró que las tres especies de roedores estudiadas consumen restos vegetales. La alta proporción de tejidos vegetales para estas tres especies puede estar asociado a la fácil obtención de energía para su mantenimiento, en comparación con una dieta basada en proteínas (Suárez 1994) y a la disponibilidad del recurso en el ambiente. Es de esperar que estas especies de roedores aprovechen los recursos disponibles de los lugares donde habitan o se refugian. Así, la familia más importante fue Poaceae, encontrándose en los cuatro sitios de muestreo y en la dieta de las tres especies evaluadas (Tabla 3; Apéndice 3), además de varias especies de dicotiledóneas. Sin embargo, no se alimentan exclusivamente de ellos cuando estaban presentes otros ítems disponibles, como micorrizas y artrópodos como se reportó para las tres especies; pero para *O. microtis* únicamente en SAF simple, aunque estas categorías estaban presentes en SAF complejo y en bosque.

Tabla 4. Coeficiente de variación (*CV*) calculado para cada categoría alimenticia en las especies.

Especies	RVe		Mic	Art		Sem	Esp	T.V.M	Otros
	Dic	Mon		Adu	Lar				
Oligoryzomys microtis	1.19	0.91	1.73	1.73			1.61	1.73	0.99
Euryoryzomys nitidus	0.93	0.46	2.00	1.20	2.00	1.20	1.28	1.16	0.59
Akodon dayi	0.07	0.05	0.83	0.20			0.99	0.36	0.25

RVe = Restos vegetales; Dic = Dicotiledóneas; Mon = Monocotiledóneas Mic = Micorrizas; Art = Artrópodos; Adu = Adultos; Lar = Larvas; Sem = Semillas; Esp = Espiguillas; T.V.M = Tejido Vascular (Morfotipos), Otros.

El género *Oligoryzomys* es considerado principalmente granívoro en estaciones secas, mientras que en estaciones húmedas su dieta consiste en follaje y ocasionalmente artrópodos (Spotorno *et al.* 2000). Nuestro estudio no realizó una comparación entre estaciones húmedas o secas; sin embargo, por los altos porcentajes de restos vegetales encontrados la dieta *O. microtis* es considerada herbívora para la época del estudio. Para el caso de *Akodon dayi*, reportes previos consideran al género *Akodon* principalmente insectívoro (Vorontsov 1961; Solari 2007; Suarez y Bonaventura 2001; Polop *et al.* 2013). Sin embargo, la presencia de restos vegetales de dicotiledóneas y monocotiledóneas observadas en *A. dayi* concuerda con reportes para otras especies del género, que complementan su dieta con el consumo de hojas (Pearson y Pearson-Ralph 1978; Brandan 1995; Giannoni *et al.* 2005; Silva 2005); además nosotros reportamos el consumo de micorrizas *Glomus fasciculatum* y *Glomus* sp. pero solamente en bosque.

Respecto al consumo de artrópodos, se evidenciaron mayores valores en el orden Coleoptera para las especies *A. dayi* y *E. nitidus* y un mayor consumo del orden Hymenoptera (familia Formicidae) en *O. microtis*. Estudios previos en la dieta de los géneros *Euryoryzomys* y *Oligoryzomys* reportaron el consumo de artrópodos Hymenoptera, Orthoptera, Araneae, larvas de Lepidoptera, larvas de Coleoptera e Hymenoptera, entre otros (Pinotti 2005; Siqueira 2013; Cervantes 2014). Reportes previos sugieren que miembros de las tribus de Akodontini (al que *Akodon dayi* corresponde), y Oryzomyini (que agrupa a *Oligoryzomys microtis* y *Euryoryzomys nitidus*, entre otros) consumen primordialmente insectos (Dorst 1972; Pizzimenti y De Salle 1980; Meserve 1981; Ellis *et al.* 1994; Noblecilla-Huiman 2008; Noblecilla y Pacheco 2012; Polop *et al.* 2015). Sin embargo, nuestro estudio sugiere que, si bien los artrópodos forman parte de la dieta de estas especies, estos no son elementos exclusivos ni mayoritarios.

En este estudio no se hizo un relevamiento de artrópodos. Sin embargo, de acuerdo con las características de los sistemas de producción, se espera que el SAF simple-monocultivo con sombra temporal, SAF complejo y bosque (con alto porcentaje de sombra a la altura del piso) presenten mayor abundancia de artrópodos. Esto explicaría el elevado porcentaje de artrópodos ingeridos en la dieta de las tres especies de roedores. Cabana (2016) reportó una mayor abundancia de los grupos Coleoptera, Hemiptera e Hymenoptera en sistemas de cultivos tradicionales. En este estudio Coleoptera e Hymenoptera fueron los más consumidos en SAF simple-monocultivo.

También se reportó la presencia de esporocarpos de micorrizas en las tres especies de roedores sigmodontinos evaluados. Otros estudios reportaron esta categoría en roedores oryzomyinos de la Amazonía (Janos *et al.* 1995) y en bosques montanos (Noblecilla y Pacheco 2012; Cervantes 2014). En este estudio no se encontraron micorrizas durante la colecta general de plantas; no obstante, al igual que los artrópodos se podría esperar que sitios con un alto porcentaje de sombra, como SAF complejo y bosque, presenten mayor abundancia de hongos. Esto explicaría la mayor cantidad de esporocarpos e hifas encontrados en la dieta de *A. dayi* y *E. nitidus* en dichos sitios, pero no explicaría la presencia de éstos en los restos estomacales de *O. microtis* en SAF simple-monocultivo.

La alta presencia de restos vegetales en la dieta de estas tres especies, puede deberse más a un proceso fisiológico que de dieta, debido a que la tasa de digestibilidad de restos vegetales es menor que el de semillas y frutos. El aparato digestivo de los roedores está adaptado para una alimentación a base de plantas, ya que digieren la celulosa en el ciego, donde se da lugar a la fermentación microbiana; además de la presencia de la cecotrofia, donde expulsan contenidos del intestino a medio digerir y los vuelven a ingerir para hacer una segunda digestión (Megías *et al.* 2016). Conectar la morfología del estómago con la dieta en los roedores es una práctica común (Vorontsov 1961). Sin embargo, este enfoque reduccionista está poco respaldado por datos y puede conducir a conclusiones sesgadas. Por ello, debe evitarse llegar a conclusiones demasiado generalizadas sin tener en cuenta otras partes importantes del aparato digestivo (Pardiñas *et al.* 2020). Otros autores concuerdan que la variación en la dieta entre especies está relacionada con la morfología del roedor, debido a que especies más pequeñas (más oportunistas) consumen una dieta rica en energía, principalmente insectos, mientras que especies más grandes en tamaño (menos oportunistas) consumen mayormente vegetación (Pizzimenti y De Salle 1980; Ellis *et al.* 1994; Noblecilla-Huiman 2008). Sin embargo, en el presente estudio, se pudo ver que la misma especie puede comportarse como más especialista o más generalista, dependiendo de la disponibilidad de alimento en al ambiente aprovechando incluso, ítems más proteolíticos (insectos) cuando éstos están presentes.

Respecto a la presencia de semillas en la dieta, no se detectaron en el aparato digestivo de las especies estudiadas (aunque sí se determinó su presencia en los diferentes cultivos muestreados). Sólo se reportó la presencia de semillas de *Polygonum* sp. en *E. nitidus* en SAF intermedio y SAF complejo, a pesar de que reportes previos para el género lo categorizan como frugívoro-granívoro (Pinotti *et al.* 2011; Paglia *et al.* 2012).

La dieta poco amplia se relaciona con el valor de importancia del recurso, que a su vez estaría relacionada con el grado de perturbación del sitio, esperando una mayor disponibilidad de recursos alimenticios en los sistemas agroforestales (SAFs) intermedios/complejos de cacao (perturbación intermedia; Connell 1978). La evaluación de los hábitos alimenticios mediante la amplitud de nicho trófico mostró que, tanto *A. dayi* como *O. microtis,* tienen una dieta amplia en SAF simple-monocultivo y bosque y menos amplia en SAF complejo para *O. microtis*, debido a que sólo se hallaron restos vegetales en sus contenidos estomacales.

Sin embargo, para *E. nitidus* se observó una dieta amplia en SAF simple-monocultivo y SAF complejo; mientras que, en parcelas SAF intermedio y bosque, *E. nitidus* presenta una menor amplitud trófica, catalogándose como especialista. Estos resultados no encajarían con la predicción realizada; teniendo que ser respuestas conductuales y de preferencia de recursos los que explique estos resultados. Así, en SAF simple-monocultivo y SAF complejo, estaría aprovechando los recursos disponibles cercanos a sus refugios sin invertir mucho gasto energético para su obtención. Por otro lado, los bajos valores obtenidos por la amplitud de nicho trófico en *E. nitidus* se explican con la dieta especializada en la familia Cyperaceae en el SAF intermedio y una dieta basada en la familia Papilionaceae y Polygonaceae en el bosque (Tabla 3), aunque estos resultados deben ser tomados con cuidado, ya que solo se pudieron evaluar dos individuos de esta especie en cada tipo de hábitat. Por ello, los resultados obtenidos pueden ser reflejo más de una "preferencia individual" o una característica del grupo.

Las medidas de sobreposición de nicho presentaron un rango con valores bajos entre las tres especies lo que sugiere que no hay competencia por los recursos entre ellas, o que, debido a una competencia interespecífica, se presenta una diferenciación de los ítems consumidos. Sin embargo, debido al bajo número de capturas de especies por tipo de cultivo, no se pudo diferenciar la dieta por hábitat. Un análisis con mayor número de muestras es necesario para confirmar nuestros resultados.

La dieta de estas tres especies de roedores, para el periodo de transición seca-húmeda en Alto Beni es diversa, y la selección de su alimento esta posiblemente relacionada con la disponibilidad de los recursos alimenticios presentes en cada tipo de parcela. SAF simple-monocultivo presenta una mayor cantidad de plantas herbáceas a nivel del suelo, a diferencia de SAF complejo y bosque, donde al haber una mayor proporción de hojarasca, también hay una menor proporción de hierbas. Según Reichman (1977) la selección nutricional es uno de los factores que determina las preferencias dietéticas en los roedores. Así, considerando los requerimientos energéticos y nutricionales de estas especies, la disponibilidad de ítems energéticamente más rentables (tallos y hojas de dicotiledóneas y monocotiledóneas) parece ser la responsable de un mayor o menor nicho trófico. Por lo tanto, podemos concluir que estas tres especies de roedores presentan diferentes tipos de hábitos alimenticios dependiendo del ambiente donde se encuentran: *O. microtis* es herbívoro-omnívoro, se califica como generalista en parcelas SAF simple-monocultivo y en el bosque y menos generalista en SAF complejo. *Euryoryzomys nitidus* es predominante herbívoro-omnívoro, se califica como generalista en parcelas SAF simple-monocultivo y menos generalista en SAF complejo; especialista en parcelas SAF intermedio y en el bosque intervenido. *Akodon dayi* presenta una dieta herbívora-insectívora, es considerada generalista en parcelas SAF simple-monocultivo y en el bosque intervenido.

Nuestro estudio señala que la dieta de estos roedores depende de la disponibilidad de alimento encontrado en su hábitat. Sin embargo, cuando existan otros recursos disponibles estos aprovecharan para incluirlos en su dieta, presentando un comportamiento oportunista con relación a la presencia de ítems alimenticos. Se deben profundizar estudios de dieta de otras especies de roedores, realizando muestreos estacionales en sistemas agroforestales, tomando en cuenta épocas reproductivas, sexo y edad para comparar con los resultados obtenidos en este estudio.

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Apéndice 1

Lista de especies de plantas colectadas en la zona de estudio, incluyendo el número de individuos colectados y su porcentaje relativo. Se presenta el número de plantas colectadas en cada tipo de sistema agroforestal y bosque.

Familia	Especie	Forma de crecimiento	Nº total de individuos colectados (%)	SAF Simple	SAF intermedio	SAF complejo	Bosque
Alstroemeriaceae	*Bomarea* sp.	Herbácea	5 (0.21)	5 (0.93)			
Amaranthaceae	*Iresine* sp.	Arbustiva	11 (0.47)		4 (0.76)	7 (1.17)	
	Iresine diffusa	Herbácea	22 (0.93)				22 (3.14)
	Alternanthera flavescens	Herbácea	12 (0.51)				12 (1.71)
	Amaranthaceae sp.	Herbácea	22 (0.93)	22 (4.09)			
Araceae	*Philodendron* sp.	Herbácea	2 (0.08)		2 (0.38)		
	Anthurium sp.	Herbácea	24 (1.02)		8 (1.53)	16 (2.68)	
Araliaceae	*Hydrocotyle* sp.	Herbácea	12 (0.51)	12 (2.23)			
Arecaceae	*Astrocaryum murumuru*	Arbórea (plántula)	8 (0.34)				8 (1.14)
Asclepiadaceae	*Asclepiadaceae* sp.	Herbácea	36 (1.53)		24 (4.60)	12 (2.01)	
Asteraceae	*Bidens andicola*	Herbácea	48 (2.04)	12 (2.23)			36 (5.14)
	Conyza bonariensis	Herbácea	141 (5.98)	25 (4.65)	21 (4.02)	44 (7.36)	51 (7.29)
	Eupatorium sp.	Herbácea	104 (4.41)	18 (3.35)	30 (5.75)	36 (6.02)	20 (2.86)
	Pseudelephantopus spiralis	Herbácea	27 (1.15)	27 (5.02)			
Blechnaceae	*Blechnum* sp.	Helecho	9 (0.38)	4 (0.74)	5 (0.96)		
Commelinaceae	*Callisia repens*	Rastrera	18 (0.76)	18 (3.35)			
Convolvulaceae	*Ipomoea* sp.	Herbácea	11 (0.47)	2 (0.37)			9 (1.29)
Costaceae	*Costus scaber*	Herbácea	55 (2.33)	12 (2.23)	14 (2.68)	29 (4.85)	
Cyperaceae	*Cyperus chalaranthus*	Herbácea	96 (4.07)		31 (5.94)	65 (10.87)	
	Cyperus friburgensis	Herbácea	57 (2.42)	22(4.09)			35 (5.00)
	Cyperus sp.	Herbácea	34 (1.44)	8 (1.49)	26 (4.98)		
Dioscoreaceae	*Dioscorea* sp.	Liana	15 (0.64)				15 (2.14)
Euphorbiaceae	*Acalypha* sp.	Herbácea	13 (0.55)	13 (2.42)			
	Acalypha stricta	Herbácea	32 (1.36)	17 (3.16)			15 (2.14)
	Acalypha arvensis	Herbácea	85 (3.60)	19 (3.53)	13 (2.49)	21 (3.51)	32 (4.57)
	Alchornea sp.	Arbórea (plántula)	5 (0.21)		3 (0.57)	2 (0.33)	
	Cnidoscolus sp.	Arbustiva	9 (0.38)		3 (0.57)	6 (1.00)	
Fabaceae	*Bauhinia* sp.	Arbórea (plántula)	11 (0.47)		2 (0.38)	3 (0.50)	6 (0.86)
	Kudan pueraria phaseoloides	Herbácea	53 (2.25)	16 (2.97)	37 (7.09)		
	Senna sp.	Arbustiva	6 (0.25)		3 (0.57)	3(0.50)	
	Schizolobium parahypa	Arbórea (plántula)	4 (0.17)		2 (0.38)	2 (0.33)	
Iridaceae	*Iridaceae* sp.	Herbácea	67 (2.76)		25 (4.79)	42 (7.02)	
Malpighiaceae	*Stigmaphyllon cardiophyllum*	Liana	16 (0.66)	16 (2.97)			
Malvaceae	*Theobroma cacao*	Arbórea (plántula)	17 (0.70)	7 (1.30)	4 (0.77)	6 (1.00)	
	Sida rhombifolia	Arbustiva	11 (0.47)	4 (0.74)			7 (1.00)
	Sterculia apetala	Arbórea (plántula)	6 (0.25)				6 (0.86)
Melastomataceae	*Melastomataceae* sp.	Herbácea	42 (1.78)				42 (6.00)
Myrtaceae	*Myrcia* sp.	Arbustiva	3 (0.13)	3 (0.56)			
Papilionaceae	*Desmodium* sp.	Herbácea	144 (6.11)	15 (2.79)	31 (5.94)	16 (2.68)	82 (11.71)
Phytolaccaceae	*Petiveria* sp.	Arbustiva	4 (0.17)				4 (0.57)
Piperaceae	*Piper aduncum*	Arbórea (plántula)	4 (0.17)	1 (0.19)			3 (0.43)
Plantaginaceae	*Plantago* sp.	Herbácea	17 (0.72)	17 (3.16)			
Poaceae	*Axonopus compressus*	Herbácea	45 (1.91)		23 (4.41)	22 (3.68)	
	Imperata sp.	Herbácea	84 (3.56)	20 (3.72)	27 (5.17)	37 (6.19)	
	Leptochloa virgata	Herbácea	76 (3.22)	32 (5.95)			44 (6.29)

Apéndice 1 continuación...

Familia	Especie	Forma de crecimiento	Nº total de individuos colectados (%)	SAF Simple	SAF intermedio	SAF complejo	Bosque
	Oplismenus hirtellus	Herbácea	75 (3.18)		25 (4.79)	50 (8.36)	
	Olyra sp.	Herbácea	56 (2.37)		30 (5.75)	26 (4.35)	
	Paspalum conjugatum	Herbácea	21 (0.89)	21 (3.90)			
	Paspalum paniculatum	Herbácea	154 (6.53)	35 (6.51)	27 (5.17)	55 (9.20)	37 (5.29)
	Paspalum sp.	Herbácea	15 (0.64)		15 (2.87)		
	Sorghum arundinaceum	Herbácea	53 (2.25)				53 (7.57)
	Poaceae sp1.	Herbácea	47 (1.99)	16 (2.97)	31 (5.94)		
	Poaceae sp2.	Herbácea	20 (0.85)	20 (3.72)			
Polygonaceae	*Polygonum* sp.	Herbácea	153 (6.49)	13 (2.42)	23 (4.41)	75 (12.54)	42 (6.00)
	Triplaris americana	Arbórea (plántula)	5 (0.21)				5 (0.71)
	Campyloneurum sp.	Helecho	30 (1.27)	9 (1.67)	12 (2.30)	9 (1.51)	
Pteridaceae	*Adiantum* sp.	Helecho	35 (1.48)	7 (1.30)	8 (1.53)	5 (0.84)	15 (2.14)
Ranunculaceae	*Thalictrum* sp.	Herbácea	30 (1.27)				30 (4.29)
Rubeacea	*Borreria* sp.	Herbácea	10 (0.42)	10 (1.86)			
Sapindaceae	*Serjania deltoidea*	Liana	30 (1.27)	9 (1.67)			21 (3.00)
	Paullinia alata	Liana	28 (1.19)				28 (4.00)
Solanaceae	*Cestrum* sp.	Arbustiva	5 (0.21)		2 (0.38)	3 (0.50)	
	Lycianthes asarifolia	Herbácea	12 (0.51)	12 (2.23)			
	Solanum sp.	Arbustiva	7 (0.30)	4 (0.74)			3 (0.43)
Thelypteridaceae	*Macrothelypteris torresiana*	Helecho	15 (0.64)	7 (1.30)			8 (1.14)
	Thelypteris sp.	Helecho	8 (0.34)		4 (0.77)	4 (0.67)	
Tiliaceae	*Triumfetta* sp.	Arbustiva	2 (0.08)		2 (0.38)		
Urticaceae	*Cecropia concolor*	Arbórea (plántula)	4 (0.17)				4 (0.57)
	Myriocarpa stipitata	Arbustiva	5 (0.21)				5 (0.71)
	Urera caracasana	Arbórea (plántula)	13 (0.55)	6 (1.12)	5 (0.96)	2 (0.33)	
	Urera sp.	Arbustiva	2 (0.08)	2(0.37)			
			2358 (100)	538 (100)	522 (100)	598 (100)	700 (100)

SAF simple = Sistema agroforestal simple-monocultivo; SAF intermedio = Sistema agroforestal intermedio; SAF complejo = Sistema agroforestal complejo; Bosque = Bosque secundario.

Apéndice 2

Composición de la dieta de tres especies de roedores sigmodontinos en los diferentes sistemas de producción de cacao para la época de transición húmeda-seca. Se muestra la ocurrencia de individuos y frecuencia en porcentaje (en paréntesis) en cada sitio de muestreo.

Restos Vegetales	**ITEMS**	**Abrev**	**Partes**	**SAF simple**	**Bosque**	**SAF simple**	**SAF intermedio**	**SAF complejo**	**Bosque**	**SAF simple**	**SAF complejo**	**Bosque**
				Akodon dayi		***Euryoryzomys nitidus***				***Oligoryzomys microtis***		
Clase: Dicotyledoneae				*n* = 5	*n* = 5	*n* = 6	*n* = 2	*n* = 3	*n* = 2	*n* = 31	*n* = 4	*n* = 6
Amaranthaceae	*Amaranthaceae* sp.*	AMAt	Tallo								8 (2.22)	
	Iresine diffusa.	IDIt	Tallo				16 (10.56)	4 (1.48)				
Araliaceae	*Hydrocotyle* sp.	HYDh	Hoja	26 (5.78)								
		HYDt	Tallo							132 (4.73)		
Asclepiadaceae	*Asclepiadaceae* sp.*	ASCt	Tallo				14 (7.78)		4 (2.22)	19 (0.68)	8 (2.22)	
Convolvulaceae	*Ipomoea* sp.	IPOt	Tallo			7 (1.30)				36 (1.29)		63 (11.67)
		IPOh	Hoja							51 (1.83)		
Euphorbiaceae	*Acalypha arvensis*	AARh	Hoja						16 (8.89)	69 (2.47)		
	Acalypha stricta	ASTh	Hoja	5 (1.11)	37 (8.22)							
		ASTt	Tallo						22 (12.30)	86 (3.08)		
	Acalypha sp.	ACAt	Tallo			2 (0.37)						
		ACAh	Hoja							74 (2.65)		
Fabaceae	Kudan pueraria phaseoloides	KPPh	Hoja			8 (1.48)						
Plantaginaceae	*Plantago* sp.	PLAh	Hoja			25 (4.63)						
Papilionaceae	*Desmodium* sp.	DESh	Hoja						60 (33.33)			
Piperaceae	*Piper aduncum*	PADh	Hoja									47 (8.70)
Polygonaceae	*Polygonum* sp.	POLt	Tallo	10 (2.22)								33 (6.11)
Rubiaceae	*Borreria* sp.	BORt	Tallo							54 (1.94)		
Solanaceae	*Solanum* sp.	SOLt	Tallo									10 (1.85)
		SOLh	Hoja							72 (2.58)		
Clase: Monocotyledoneae												
Alstroemeriaceae	*Bomarea* sp.	BOMh	Hoja			6 (1.11)				147 (5.27)		
Araceae	*Anthurium* sp.	ANTh	Hoja		27 (6.00)		16 (8.89)	12 (4.44)		27 (0.97)	54 (15.0)	
Commelinaceae	*Callisia repens*	CREt	Tallo							114 (4.09)		
Costaceae	*Costus scaber*	CSCh	Hoja							114 (4.09)		
		CSCt	Tallo	25 (5.56)	7 (1.56)					11 (0.39)	35 (9.72)	
Cyperaceae	*Cyperus chalaranthus*	CCHt	Tallo				28 (15.56)	8 (2.96)				
Poaceae	*Axonopus compressus*	ACOt	Tallo							51 (1.83)	76 (21.11)	
	Imperata sp.	IMPt	Tallo								67 (18.61)	
	Oplismenus hirtellus	OHIh	Hoja	14 (3.11)								
		OHIt	Tallo				7 (3.89)		25 (13.89)		60 (16.67)	
	Paspalum conjugatum	PCOt	Tallo							124 (4.44)		
		PCOh	Hoja	8 (1.78)	28 (6.22)					23 (0.82)		
	Paspalum paniculatum	PPAt	Tallo	5 (1.11)	6 (1.33)					116 (4.16)		108 (20.0)
		PPAh	Hoja							59 (2.11)		
	Paspalum sp.	PASt	Tallo			34 (6.30)	7 (3.89)		6 (3.36)			
	Poaceae sp1. *	PO1h	Hoja			3 (0.56)				87 (3.12)		
	Poaceae sp2. *	PO2h	Hoja			15 (2.78)				65 (2.33)		
	Sorghum arundinaceum	SARh	Hoja	11 (2.44)								
		SARt	Tallo									42 (7.78)
Semillas												

Apéndice 2 continuación...

Restos Vegetales	ITEMS	Abrev	Partes	SAF simple	Bosque	SAF simple	SAF intermedio	SAF complejo	Bosque	SAF simple	SAF complejo	Bosque
				Akodon dayi		***Euryoryzomys nitidus***				***Oligoryzomys microtis***		
Clase: Dicotyledoneae												
Polygonaceae	*Polygonum* sp.	POLs	Semilla				6 (5.56)	4 (1.48)				
Espiguillas												
Clase: Monocotyledoneae												
Cyperaceae	Cyperus chalaranthus	CCHl	Lemma			13 (2.41)						
		CCHp	Pálea			7 (1.30)						
Poaceae	*Axonopus compressus*	ACOp	Pálea			8 (1.48)						
	Paspalum conjugatum	PCOes	Espiguilla	22 (4.89)	15 (3.33)					6 (0.22)		123 (22.78)
		PCOg	Gluma	4 (0.89)								
		PCOp	Pálea	5 (1.11)								
	Paspalum paniculatum	PPAes	Espiguilla	23 (5.11)			22 (12.20)					
		PPAg	Gluma	17 (3.78)	2 (0.44)							
		PPAp	Pálea	12 (2.67)								
		PPAl	Lemma	8 (1.78)								
		PPAa	Arista	5 (1.11)								
	Paspalum sp.	PASes	Espiguilla			93 (17.22)						
Micorrizas												
Clase: Glomeromycetes												
Glomerales	*Glomus clavisporum*	GCLe	Esporocarpo					96 (35.56)				
	Glomus fasciculatum	GFAe	Esporocarpo		46 (10.22)							
		GFAhi	Hifas		25 (5.56)							
	Glomus macrocarpum	GMAe	Esporocarpo							175 (6.27)		
		GMAhi	Hifas							187 (6.70)		
	Glomus sp1.	GL1e	Esporocarpo		32 (7.11)							
		GL1hi	Hifas		21 (4.67)							
	Glomus sp2.	GL2e	Esporocarpo	12 (2.67)						147 (5.27)		
		GL2hi	Hifas	20 (4.44)						141 (5.05)		
Artrópodos Adultos												
Clase: Insecta	Coleóptera	COL		48 (10.67)	14 (3.11)	124 (22.96)		58 (21.48)				
	Díptera	DIP		28 (6.23)	28 (6.22)							
	Dyctioptera	DYC		20 (4.44)								
	Formicidae	FOR			55 (12.22)					33 (1.18)		
	Hemiptera	HEM								27 (0.97)		
	Hymenoptera	HYM		61 (13.56)	33 (7.33)	20 (3.70)		37 (13.70)		58 (2.08)		
	Lepidoptera	LEP		13 (2.89)								
Artrópodos larvas												
	Hymenoptera larvas	HYL				39 (7.22)						
Tejido Vascular												
	Morfotipo	MOR		22 (4.89)	37 (8.23)	6 (1.11)		7 (2.59)		79 (2.59)		
Otros	Chlorophyta	CHL	Alga									24 (4.44)
	Pelos	PEL		6 (1.33)	8 (1.78)	42 (7.78)	19 (10.56)	11 (4.07)	13 (7.22)	136 (4.87)	17 (4.72)	37 (6.85)
	Piedras	PIE		6 (1.33)	12 (2.67)	18 (3.33)	16 (8.89)	13 (4.81)	6 (3.33)	77 (2.76)	6 (1.67)	20 (3.70)
	Restos de avena	RAV		7 (1.56)	6 (1.33)	25 (4.63)	16 (8.89)	7 (2.59)	17 (9.44)	93 (3.34)	11 (3.06)	12 (2.22)
	Bolsa plástica	BPL								7 (0.49)	8 (2.22)	
	Indeterminado	IND		7 (1.56)	11 (2.44)	45 (8.33)	6 (3.33)	13 (4.84)	11 (6.11)	93 (3.34)	10 (2.78)	21 (3.89)

Apéndice 3

Índice del valor de importancia de recursos del orden/familias consumidos por los roedores *Akodon dayi*, *Euryoryzomys nitidus* y *Oligoryzomys microtis*. Se muestra el uso de recurso (Pxi) y el índice de valor de importancia de recursos (IVIR) en cada sitio de muestreo, se marcan con * los valores mayores a 0.1 y los resultados de IVIR mayores a 0.1 se encuentran resaltados con negrillas.

	SAF simple				**SAF intermedio**		**SAF complejo**			**Bosque**			
	O.mi	*E.ni*	*A.da*		*E.ni*		*O.mi*	*E.ni*		*O.mi*	*E.ni*	*A.da*	
Orden/ Familia	Pxi	Pxi	Pxi	**IVIR** Pxi		**IVIR** Pxi	Pxi		**IVIR** Pxi	Pxi	Pxi		**IVIR**
Amaranthaceae					0.092	0.092	0.022	0.015	0.037				
Araliaceae	0.047		0.058	0.105									
Asclepiadaceae	0.007			0.007	0.081	0.081	0.022		0.022		0.022		0.022
Convolvulaceae	0.031	0.013		0.044						0.117			0.117
Euphorbiaceae	0.082	0.004	0.011	0.097							0.211*	0.074	***0.285***
Fabaceae		0.015		0.015									
Plantaginaceae		0.046		0.046									
Papilionaceae											0.333*		***0.333***
Piperaceae										0.087			0.087
Polygonaceae			0.022	0.022	0.035	0.035		0.015	0.015	0.061		0.105	0.166
Rubiaceae	0.019			0.019									
Solanaceae	0.026			0.026						0.019			0.019
Alstroemeriaceae	0.053	0.011		0.064									
Araceae	0.010			0.010	0.092	0.092	0.150	0.044	0.194			0.054	0.054
Commelinaceae	0.041			0.041									
Costaceae	0.045		0.056	0.100			0.097		0.097			0.014	0.014
Cyperaceae		0.037		0.037	0.162	***0.162***		0.030	0.030				
Poaceae	0.190	0.283*	0.298*	***0.771***	0.208*	***0.208***	0.564*		***0.564***	0.506*	0.172	0.101	***0.779***
Glomerales	0.233*		0.071	***0.304***				0.356*	***0.356***			0.247*	***0.247***
Coleóptera		0.230*	0.107	***0.336***				0.215*	***0.215***			0.028	0.028
Díptera			0.062	0.062								0.056	0.056
Dyctioptera			0.044	0.044									
Formicidae	0.012			0.012								0.109	0.109
Hemiptera	0.010			0.010									
Hymenoptera	0.021	0.037	0.136	***0.193***				0.137	0.137			0.066	0.066
Lepidoptera			0.029	0.029									
Hymenoptera pupas		0.072		0.072									
Tejido Vascular	0.028	0.011	0.049	0.088				0.026	0.026			0.074	0.074
Otros	0.146	0.241*	0.058	***0.444***	0.329*	***0.329***	0.144	0.163	***0.307***	0.211*	0.261*	0.074	***0.546***

SAF simple = Sistema agroforestal simple monocultivo; SAF intermedio = Sistema agroforestal intermedio; SAF complejo = Sistema agroforestal complejo; Bosque = Bosque secundario. O.mi = *Oligoryzomys microtis*; E.ni = *Euryoryzomys nitidus*; A.da = *Akodon dayi*.

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Woody plant encroachment drives habitat loss for a relict population of a large mammalian herbivore in South America

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Woody plant encroachment (WPE) is reshaping the physiognomy of grasslands and savannahs worldwide. At the same time, this habitat conversion is accelerating the loss of associated biodiversity. In general, studies on WPE have focused on abiotic factors, singly or in combination, that trigger this phenomenon. Despite its ecological relevance, very few studies have tackled the effects of WPE-spurred habitat transformation on animal species dependent on relatively open areas such as grasslands and savannas for survival. We studied a relict and almost extinct population of large, herbivorous guanacos (*Lama guanicoe*) in the Gran Chaco region, Santa Cruz department, Bolivia. We tested whether guanacos were using habitats (at particular and distinct stages of WPE) in relation to their availability. Although this species is considered a generalist herbivore. We tested variation in habitat use focusing on two spatial scales. First, at the landscape level, we performed aerial surveys. Second, at the fine scale, we tracked six groups of guanacos for twenty months and documented the various habitats used within their approximate home ranges. At both scales, we performed a Manly-Chesson's index referring to the standardised proportional use of each habitat divided by the proportional availability of each, with the values for all habitats summing to 1. An index value < 1 or > 1 suggests, respectively, that a habitat is avoided or selected. We found a disproportionate use of open vegetation (scrubland and grassland) by guanacos in relation to habitat availability at both scales. In addition, the current distribution range of the species is restricted to less than 800 km^2 of the approximately 3,000 km^2 potentially available in 1998. We confirmed a contraction between 1996 and 2006 in the distribution of the local Chacoan guanaco population from the area where guanacos were first monitored towards the Kaa-Iya National Park border. Our results showed that guanacos are restricted to relatively open areas. Furthermore, the observed reduction in the area previously occupied by the species could be the beginning of a distributional shift and potential loss of the guanaco's geographic range due to habitat replacement. The latter was also reflected in a previous dietary study of this population we found that guanacos largely consumed the native grass *A. mendocina* (Poaceae), which has shrunk in distribution by 90 % in this region over a 40 year period and is gradually being replaced by an invasive forb, *Lippia* sp. Therefore, if the overall purpose on evaluating habitat use is to understand the basic requirements to sustain this population of guanacos, we need to highlight the poor quality and acute regression of the current preferred habitat. In this case, habitat structure can have a profound effect on the success of the guanaco population recovery and its long-term establishment. Therefore, we urge researchers and decision makers to look beyond the more direct human-induced pressures on the species, such as hunting, competition with domestic livestock and agricultural development and consider the importance of WPE as a direct driver for habitat loss.

El incremento de la vegetación arbustiva está reformando la fisonomía de los pastizales y sabanas a lo largo del mundo y acelerando la pérdida de la biodiversidad. En general, los estudios sobre arbustización se han focalizado en factores abióticos, actuando tanto en forma individual como combinados, que han disparado el fenómeno. A pesar de su relevancia ecológica, muy pocos estudios han enfrentado los efectos derivados de la transformación del hábitat vía arbustización, sobre especies dependientes, para su supervivencia, de áreas relativamente abiertas, tales como pastizales o sabanas. Nosotros estudiamos una población relictual y casi extinta de un gran herbívoro, el guanaco *Lama guanicoe* en la región del Gran Chaco en Bolivia. Allí pusimos a prueba la hipótesis de que los guanacos están usando hábitats (en diferentes estados de arbustización) con relación a su disponibilidad. Además evaluamos la prueba la variación en el uso del hábitat enfocado a dos escalas espaciales. Primero, a nivel de paisaje, a partir de reconocimientos aéreos. Segundo, a una escala fina, seguimos en el campo 6 grupos de guanacos durante 20 meses y registramos su uso de hábitat dentro de sus ámbitos de hogar aproximados. Para ambas escalas, aplicamos el índice de Manly–Chesson. Un valor del índice < 1 o >1 sugiere que el hábitat es evitado o seleccionado, respectivamente. Encontramos que los guanacos usan la vegetación abierta (matorral y pastizal) en forma desproporcionada en relación con la disponibilidad de los hábitats para ambas escalas de abordaje. Además, que la actual distribución geográfica de la especie está restringida a menos de 800 km^2 de los ca. 3,000 km^2 potencialmente disponibles en 1998. Confirmamos una retracción, entre 1996 y 2006 en la distribución del guanaco chaqueño a partir del área donde fue monitoreado por primera vez hacia el límite del Parque Nacional Kaa-Iya. Nuestros resultados mostraron que los guanacos están restringidos a las áreas relativamente más abiertas. Además, que la reducción observada en el área previamente ocupada por la especie podría constituir el comienzo de un cambio distribucional y una potencial pérdida de rango geográfico para el guanaco, debido al reemplazo de hábitat. Esto último sumado a que la gramínea nativa *Aristida mendocina* (Poaceae), especie preferida en la dieta del guanaco chaqueño, está siendo gradualmente reemplazada por una leñosa invasora, *Lippia* sp. Por lo tanto, si el propósito global de la evaluación del uso de hábitat es comprender los requerimientos básicos para sostener esta población de guanacos, necesitamos destacar la pobre calidad y aguda regresión de su hábitat preferido contemporáneo. En este caso, la estructura del hábitat puede tener un profundo efecto sobre el éxito de la recuperación de la población de guanaco y su sostenibilidad a largo plazo. Por lo tanto, urgimos a los investigadores y gestores a considerar la importancia de la arbustización como un factor directo conducente a la pérdida de hábitat y una amenaza inminente a la biodiversidad regional.

Keywords: Bolivia; Gran Chaco; *Lama guanicoe*; Pampas; tropical dry forest; "thicketisation" of savannahs.

Introduction

Habitat loss is most often perceived to be caused by discernibly drastic factors such as clear-cutting of forest for the expansion of agriculture (Andren 1997). In contrast, a more subtle, transformative pressure on vegetation communities is "woody plant encroachment" (WPE; Archer *et al.* 2017), also known as the "thicketisation" of grasslands (Archer *et al.* 1995). This phenomenon of WPE has increased worldwide over the past century, albeit at different rates in different continents (Sankaran *et al.* 2005; Sala and Maestre 2014; Archer *et al.* 2017; Stevens *et al.* 2017; Garcia-Criado *et al.* 2019). Despite its ecological relevance, there is a general recognition of the complexity in identifying the main causative drivers for this phenomenon; especially since variations in time, land-use history and bioclimatic zones need to be taking into account (Van Langevelde *et al.* 2003; Sankaran *et al.* 2005; Kulmatiski and Beard 2013; Archer *et al.* 2017). Furthermore, WPE-driven reshaping of the physiognomy of grasslands and savannas (Kenoyer 1929; Van Auken 2000; Scheffer *et al.* 2001; Graz 2008) has effectively resulted in their overall depletion of these habitats with associated declines in plant species richness (Ratajczak *et al.* 2012), or their degradation (Baez and Collins 2008). In addition, the specific consequences for ecosystem function and biodiversity are variable (Barger *et al.* 2011; Eldridge *et al.* 2011) from overall declines across trophic levels to expansion or reduction of specialist species ranges, among many other changes reviewed by Garcia-Criado *et al.* (2019). Furthermore, WPE could be a significant pressure on both grazing and browsing herbivores, causing perhaps reductions in forage value (Eldridge *et al.* 2011), and therefore transforming the structure of the vegetation communities that make up their habitats.

As stated by Archer *et al.* (2017) very little is known regarding specific responses of animals to WPE-driven habitat transformation. There are a few studies relating habitat transformation to different components of biodiversity such as birds (Knopf 1994; Coppedge *et al.* 2001; Skowno and Bond 2003; Coppedge 2004; Cunningham and Johnson 2006; Sirami *et al.* 2009; Block and Morrison 2010; Sirami and Monadjem 2012), arthropods (Steenkamp and Chown 1996; Blaum *et al.* 2009), and reptiles (Mendelson and Jennings 1992; Meik *et al.* 2002; Pike *et al.* 2011). However, to the best of our knowledge, there are only around a dozen specific studies on the consequences of shrub encroachment on mammals in general (Kavwelle *et al.* 2017). Examples of the latter are, specifically rodents (Blaum *et al.* 2007a; Emmons 2009; Bilney *et al.* 2010; Pardiñas *et al.* 2012; Pardiñas and Teta 2013), carnivores (Blaum *et al.* 2007b), and ungulates (Okello 2007; Kimaro *et al.* 2019). Among the latter, only a few have explored the disruption caused by WPE on mammalian species dependent on relatively open areas such as grasslands and savannas (Krogh *et al.* 2002; Blaum *et al.* 2007a).

In South America, one of the largest native mammalian herbivores, strongly associated with grasslands, with the exception of the cold forests in Tierra del Fuego (Muñoz and Simonetti 2013), is the guanaco *Lama* guanicoe (Miller *et al.* 1973; Franklin 1982, 1983; Travaini *et al.* 2007). Despite guanaco presence in four of the ten major ecoregions described in South America, the distribution range of this species has contracted by 60 % during the last century (Gonzalez *et al.* 2006). The situation is further exacerbated with local extinctions and isolation of guanaco populations within its current distribution range (Miller *et al.* 1973; Sosa and Sarasola 2005; Gonzalez *et al.* 2006; Cuellar-Soto *et al.* 2017a; Cook-Mena *et al.* 2019). Strikingly, despite the latter, the guanaco continues to be categorized as of least concern (LC) by the IUCN (Baldi *et al.* 2016). However, three (Perú, Bolivia and Paraguay) of the five countries that acknowledge this incongruity have changed the guanaco's conservation status to Endangered (EN) and Critically Endangered (CR; Cuéllar and Núñez 2009; Cartes *et al.* 2017; SERFOR 2018).

In Bolivia, we studied the relict and isolated population of around 200 Chacoan guanacos, which constitutes the north-eastern fringe of the species range (Cuéllar and Núñez 2009). At the same time, this population is restricted to an area characterized by a mosaic of vegetation in different stages of the WPE process, with variations in height (0.4 to 4 metres) and thickness (Navarro and Fuentes 1999; Pinto and Cuéllar-Soto 2017).

We tested differential use of habitats at different stages of WPE by guanacos in relation to their availability, both at a landscape and home range scale. Although guanacos are considered as generalist herbivores (Raedeke and Simonetti 1988; Puig *et al.* 2001; Puig *et al.* 2011), we hypothesized that guanacos prefer native grasslands and the early stages of encroachment together with the remaining of native grasslands over other available habitats. Finally, we hypothesised that WPE is causing contraction of potential suitable habitat for the Chacoan guanacos.

Materials and Methods

The study area extends from -19° 45′ to 20° 30′ S and from -62° 00′ to 63° 00′ W, on the fluvial megafans of the Río Grande and the Río Parapetí in the Bolivian Gran Chaco (May *et al.* 2008), in the extreme south of Santa Cruz department, Bolivia. The study area includes the southwest corner of the Kaa-Iya National Park and part of the Indigenous Isoseño Communal Land (Figure 1). The climate is predominantly semi-arid (Peel *et al.* 2007), with annual rainfall ranging from 200 to 350 mm (Taber *et al.* 1997).

We used the information on the expansion of each vegetation community from the vegetation maps produced by Pinto and Cuéllar-Soto (2017b). The latter is based on Navarro's classification of stages of WPE in the study area (open forest, thick woodland, shrubland, scrubland, grassland) according to their structure (0.40 to 4 metres), species composition and cover (Navarro and Fuentes 1999).

The total area covered by our aerial surveys (Figure 2) was the potential guanaco range. We defined the latter by taking into account: 1) earlier guanaco observations and interviews with local people (Villalba 1992; Emmons 1993; Anderson 1997; Cuéllar and Fuentes 2000), and 2) the potentially suitable habitats, including all main expansions of savannahs and relatively open vegetation on sandy soil covering around 3,000 km^2 (Cuéllar and Fuentes 2000). In addition, we compared the observations gathered in a specific area, between 1996 and 1998 (Miserendino *et al.* 1998; Weber 2000), to those collected between 2005 and 2006 to confirm retraction in part of the guanacos' local distribution range.

At the landscape level, we determined the distribution of guanacos from aerial surveys in April 1998, December 2001 and December 2004, and confirmed in subsequent aerial surveys (2008 and 2011). We used a single-engine light aircraft (Maule ML5) during peak periods of guanaco foraging activity (early morning from 6 to 8 AM) when guanacos were most likely to be visible and hence detected. We maintained a constant height of approximately 100 m above ground level at an average speed of 180 km/hr along fixed-width strip transects (450 m to each side of the aircraft), oriented north-south. We defined the "usage" of habitat as a given area at a radius of 450 m around each guanaco observation point from the plane. Determination of this area was resolved using either side of the aerial transect as a measure, together with the visibility we had from the plane. In addition, we defined as habitat availability the total area during the first aerial survey.

Figure 1. The study area is in the extreme south of the Santa Cruz department of Bolivia and less than 100km from the Paraguayan border. It is part of the Indigenous Isoseño Communal Land and includes the southwest corner of the Kaa-Iya National Park.

On a fine scale, for the purposes of analysis, we selected the information gathered for only six distinct guanaco groups tracked for twenty months (between 2007 and 2009) and recorded the habitat used within their approximate home ranges. These small groups of between two to four adults with one or two newborns or sub-adults (Table 1), remained in the same general area throughout the year. Group composition did not vary during the monitoring period. We identified groups from variations in phenotypical traits and morphological characteristics such as scars, fur colour variations in males, and group composition (Cuéllar and Noss 2014) – an approach similar to that used to identify other species with subtle differences in skin patterns, such as puma *Puma concolor* (Kelly *et al.* 2008). We used roads and trails as fixed transects crossing different habitats within the vegetation mosaic. Mean transect length, travelled on foot or on horseback, was 10.5 km (range: 7 to14 km). Locations of identified guanacos were recorded and mapped using ArcView (Environmental Systems Research Institute, Redlands, USA). Minimum home ranges (utilized habitats) were estimated using Minimum Convex Polygons (sensu Mohr 1947) and Animal Movement Analysis Extension (Hooge and Eichenlaub 1997). Using Ranges7 software (South *et al.* 2005), we determined the core area (Kernel 99 %) of the guanaco population from cumulative observations and determined it as available habitats.

At both scales [1) the landscape level, habitat within the 450 m radius buffer around each observation location versus total area surveyed with the aircraft. And 2) the fine scale, home ranges versus core area of the study population] we performed a Manly-Chesson's index referring to the standardised proportional use of each habitat divided by its proportional availability, so the values for all habitats sum to 1 (Manly *et al.* 1972; Chesson 1978). An index value < 1 or > 1 suggesting, respectively, that the habitat is avoided or selected.

Finally, we plotted the observations recorded in two periods, the first between 1996 and 1998 and the second between 2005 and 2006. Data was gathered using the

Table 1. Composition of the six groups identified and monitored, identification number, sex, newborns and sub-adults.

Group ID	Number	Male	Female	Newborn	Sub-adult
G1	5	1	3	1	0
G2	5	1	2	2	0
G3	7	1	4	2	0
G4	6	1	4	0	1
G5	1	1	0	0	0
G6	3	1	2	0	0

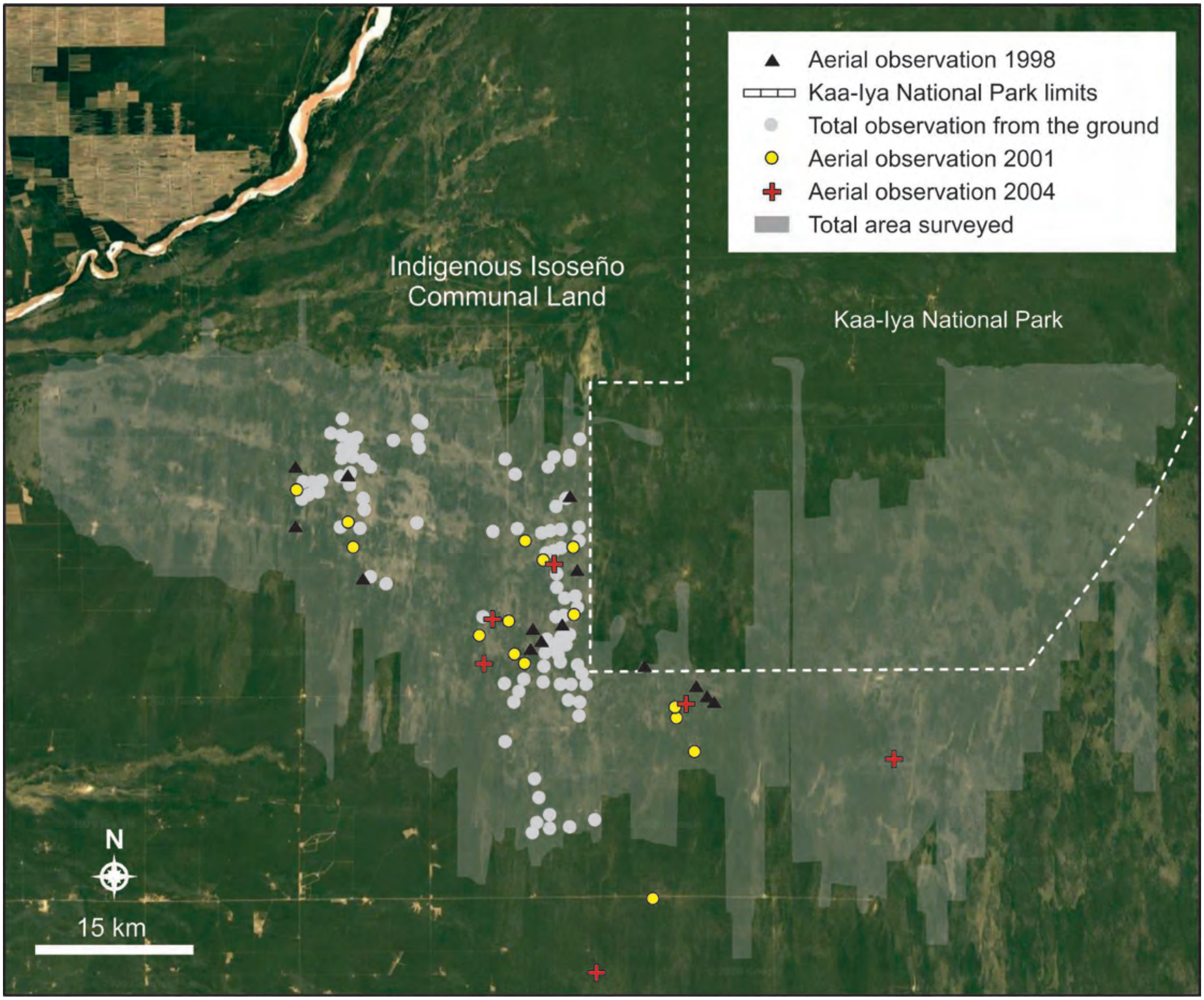

Figure 2. The total area covered by the aerial surveys. The total area covered by our aerial surveys (in grey). This area surveyed represents the potentially suitable habitats on sandy soil covering around 3,000 km^2.

same methodology (by foot or on horseback) and by the same core of observers on a map including the borders of the newly created Kaa-Iya del Gran Chaco National Park.

Results

We estimated the Chacoan guanaco range to be less than 800 km^2 from the approximately 3000 km^2 potentially available in 1998. The same broad distribution was confirmed 13 years later by subsequent aerial surveys (2001, 2004, 2008, 2011) and in 2020 by monthly reports of the Kaa-Iya National Park para-biologists and park rangers.

At a landscape level, the proportions of habitat categories available in the landscape versus proportions utilised (within a 450 m radius of observations during aerial surveys) are presented in Table 2. In addition, Manly-Chesson index values suggested consistent patterns in use of the study area by guanacos (Figure 3). Index values calculated for the three aerial surveys (1998, 2001, and 2004) were each >1 indicating that the combination of scrubland and grassland was the favoured habitat type over shrubland, thick woodland and open forest.

At a fine scale, the mean home range of these guanaco groups, which maintained constant familial compositions throughout the study period, was 24 km2 (± 14 SD; N = 6, range: 13 to 51 km^2; Cuéllar and Noss 2014). The proportions of habitat categories available within the guanaco population core area versus proportions within minimum convex polygon (MCP) – approximate home ranges– of six guanaco groups are presented in Table 3. Manly-Chesson index values were not consistent between groups and are presented in Figure 4. In fact, the index value was >1 for only two (G1 and G4) of the six groups, with a scrubland/grassland type habitat combination clearly favoured by these two groups over other available habitat types (shrubland, thick woodland and open forest). In contrast, the index value for group five (G5) suggested preference for shrubland and thick woodland. Two groups (G2 and G3) showed preference for the combination of scrubland and

Table 2. Landscape level analysis: Proportions of habitat categories available in the landscape versus proportions utilized (within a 450m radius of observations during aerial surveys).

Habitat type	Available % (1998)	Mean % habitat use	Available % (2001)	Mean % habitat use	Available % (2004)	Mean % habitat use
Open Forest	30.8	2.5	19.0	13.0	41.2	6.2
Thick woodland	10.9	2.3	15.9	7.6	11.0	3.2
Shrubland	23.0	20.8	34.1	21.9	21.9	14.5
Scrubland+Grassland	35.3	74.26	35.4	57.5	25.9	76.1

grasslands plus shrubland with the remaining group (G6) only showing avoidance for open forest.

When records from two periods were plotted, we observed a contraction in part of the local distribution towards the Kaa-Iya National park border, between 1996-1997 and 2005-2006 (Figure 5), the latter confirming the comments from local ranchers.

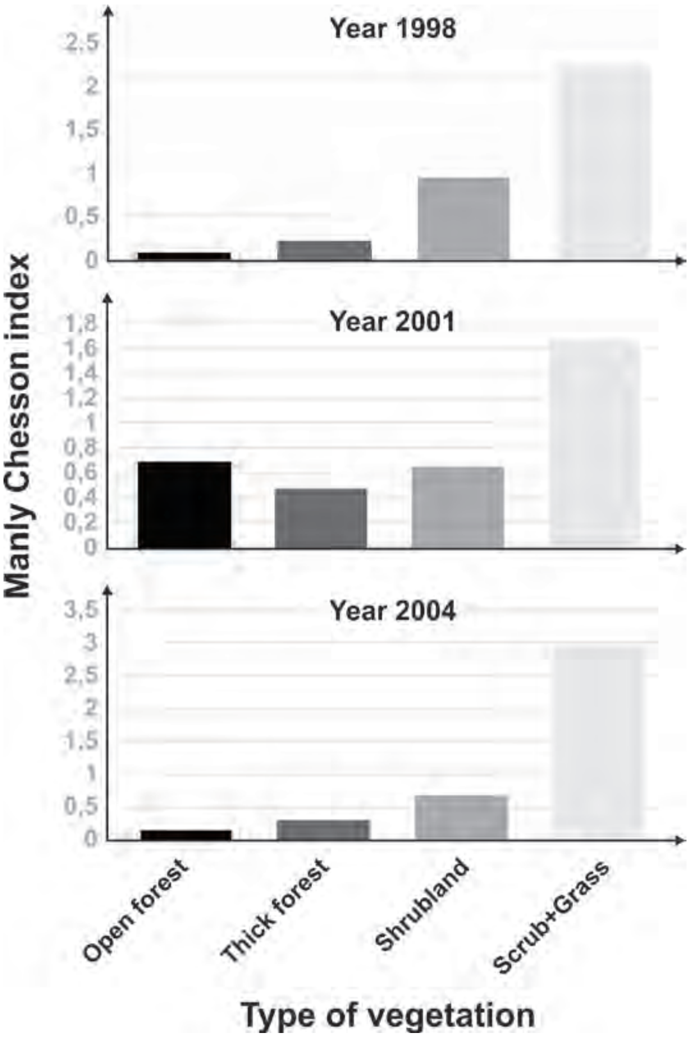

Figure 3. Manly-Chesson index values for the three aerial surveys (1998, 2001 and 2004) suggested consistent patterns in use of the study area by guanacos. Index values >1 indicates that the combination of scrubland and grassland was the favoured habitat type over shrubland, thick woodland and open forest.

Discussion

This study is the first investigation on use of habitat by a relict population of guanacos in the Bolivian Gran Chaco. First, our results supported the prediction that, at a landscape scale, guanaco showed preference to areas where the early stages of woody plant encroachment were relatively low. The latter is not surprising since a previous study showed that Chacoan guanacos are largely pastoral (Cuéllar-Soto *et al.* 2017b). However, these grassy areas, consisting mainly of communities of the native grass *Aristida mendocina* (Poaceae), are themselves disappearing due to different stages of WPE (Pinto and Cuéllar-Soto 2017), starting with the gradual replacement of *A. mendocina* by an invasive forb *Lippia* sp. (Navarro 2002). Therefore, if the overall purpose on evaluating habitat use is to understand the basic requirements to sustain this population of guanacos, we need to highlight the poor quality and acute regression of the current preferred habitat. In this case, habitat structure can have a profound effect on recovery success of the guanaco population and its long-term establishment. On one hand, the loss of suitable habitat could affect food availability for guanacos, owing to the replacement of palatable plants by unpalatable woody species and annuals as previously reported from studies in South Africa (Chambers *et al.* 1999), Australia and the United States of America (Janssen *et al.* 2004). On the other hand, effective detection of predators can be impeded by WPE through deteriorations in guanaco visibility (*e. g.* Riginos and Grace 2008; Underwood 1982). Therefore, WPE is likely to have a negative effect on the ability of guanacos and other species living in open environments, reliant on sight, to detect predators (Kunkel and Pletscher 2000; Barri and Fernández 2011; Flores *et al.* 2012). In addition, Bank *et al.* (2002) reported that puma kills on guanacos were significantly more frequent in habitat with dense cover (mainly shrubland) and suggested that guanacos' selection for open and flat terrain is a critical component of their predator avoidance strategy and long-term survival. Similarly, Owen-Smith (2008) argued that shorter grass height can reduce the predation vulnerability of wildebeest *Connochaetes taurinus* and zebra *Equus burchelli* in Africa.

Furthermore, we observed some differences at a home range scale in the use of habitat among the groups. The index values for G1, G2, G3 and G4, suggested that the combination of scrubland and grassland habitat type was favored over shrubland, thick woodland and open forest. Interestingly, those groups had the highest numbers with either a newborn or subadult as part of the family group. In contrast, G5 and G6 were groups of two couples without offspring. This latter point could raise the question as to whether habitat preference is more notably linked to reproduction and survival (Garshelis 2000), so, in effect, does our observed pattern suggest a limitation of the

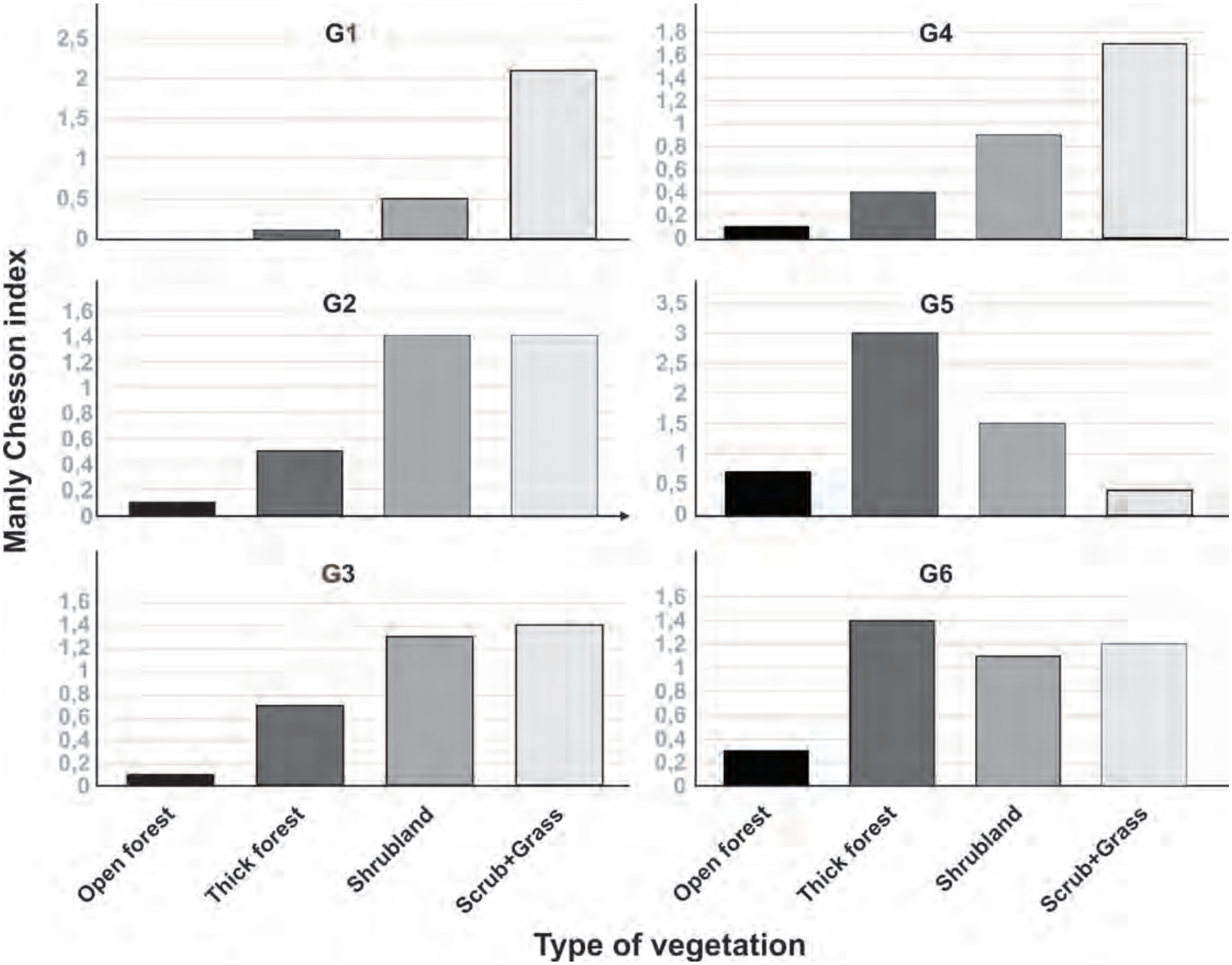

Figure 4. Manly-Chesson index values for the six groups (G1, G2, G3, G4, G5, and G6). The index value >1 for scrubland/grassland type habitat combination clearly showed that G1 and G4 favoured that available habitat types over shrubland, thick woodland and open forest. G5 suggested preference for shrubland and thick woodland, and G2 and G3 showed preference for the combination of scrubland and grasslands plus shrubland. G6 only showed avoidance for open forest.

current mosaic for supporting population growth? If true, can we assume that the guanaco population in question is under risk of early extinction? To help answer this question additional information and monitoring data acquired from recent technological advances and field equipment is required. This may involve the use of expandable GPS collars for subadults to assess individual patterns of dispersion following expulsion from the family group. However, any attempt to capture and tag Chacoan guanacos should consider the current situation of such a small and fragile population and the risk of having animals escaping into dense vegetation and or barb-wired borders of private ranches, at a risk to themselves. Given the low visibility and the small chances to encounter the guanacos, which is extremely contrasting to any other population studied on the continent (Cunazza *et al.* 1995; Baldi *et al.* 2009; Sosa and Sarasola 2005; Arzamendia *et al.* 2006; Puig *et al.* 2008; Cassini *et al.* 2009; Acebes *et al.* 2010; Burgi *et al.* 2011; Parreño *et al.* 2001; Flores *et al.* 2012; Cook-Mena *et al.* 2019; Puig *et al.* 2019), the use of horses is recommended. Furthermore, researchers should expect to invest a lot of physical effort and time, including travelling long distances

Table 3. Fine scale analysis: Proportions of habitat categories available within the guanaco population core area versus proportions within minimum convex polygon (MCP) home ranges of six guanaco groups.

Habitat type	% habitat available	MCP 1	MCP 2	MCP 3	MCP 4	MCP 5	MCP 6
Open Forest	25.0	0.0	3.0	3.7	2.3	18.9	7.9
Thick woodland	9.5	1.0	4.7	6.9	3.7	29.4	13.5
Shrubland	24.6	12.3	34.9	32.8	23.3	36.9	28.8
Scrubland+Grassland	40.7	86.5	57.3	56.3	70.5	14.6	49.5

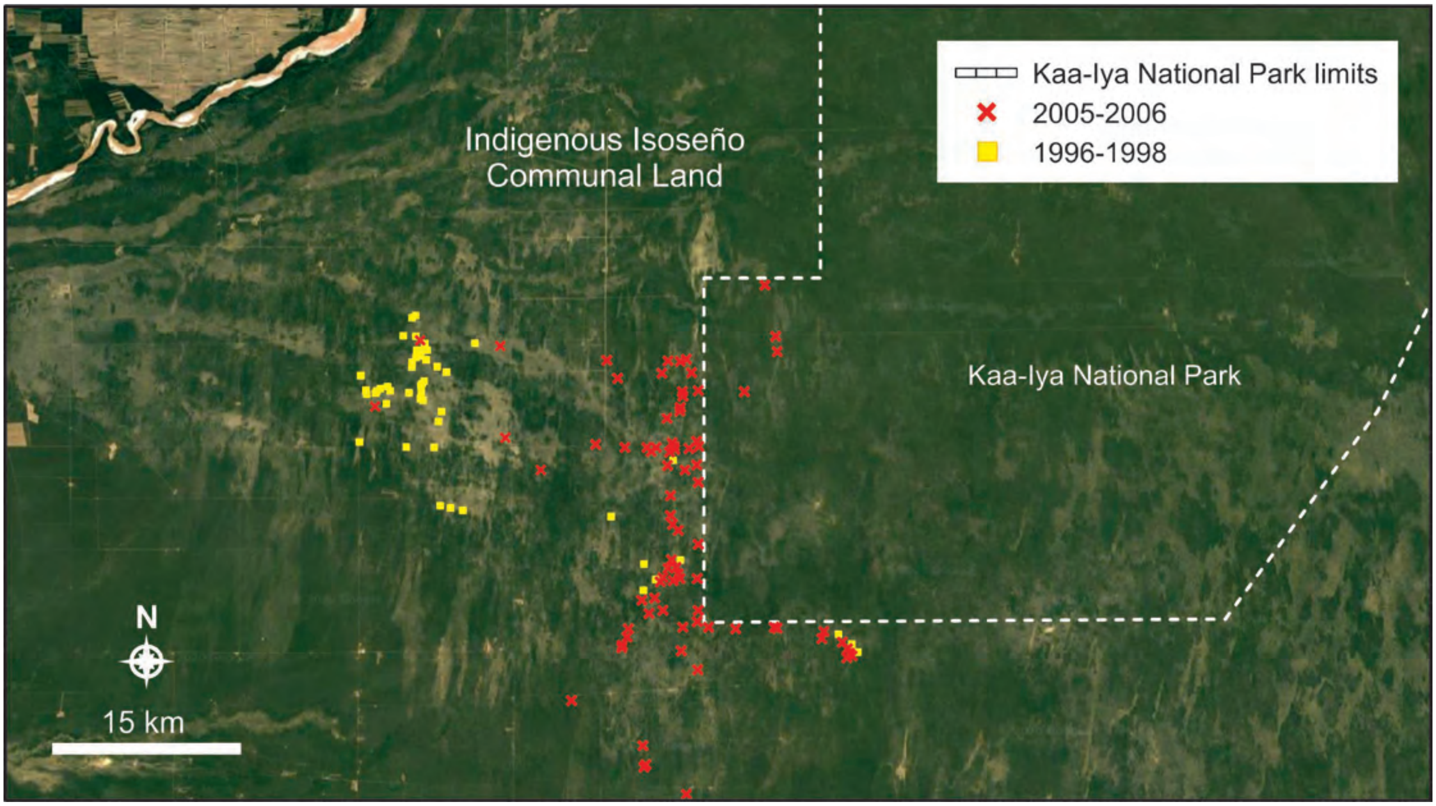

Figure 5. The comparison between the records gathered in two periods (1996-1998 and 2005-2006) showed a retraction in the distribution of the local Chacoan guanaco population towards the Kaa-Iya National Park border.

over several days and rough terrain without observing any guanacos.

In addition, on both scales, our results showed that guanacos were concentrated within the same broad range and within the most open areas, suggesting that this guanaco population is sedentary. According to Franklin and Fritz (1991) guanacos can be sedentary or migratory in response to food availability. However, there is no suitable habitat into which guanacos can expand their range unless effective management interventions are implemented on the respective ranch properties, indigenous communal lands, and a portion of the Kaa-Iya National Park currently occupied by the guanacos. At present, almost the entire guanaco population is restricted to private lands and indigenous communal land. On one hand, the private lands are mainly cattle ranches with evident degradation of pasture and invasion by woody plants (Angulo and Rumiz 2009). On the other hand, and with a more promising prospect, there has been a recently approved municipal law ("*Ley autonómica No 034/2019 ley de creación, conservación del Área de Vida del Guajukaka (guanaco) en la Zona Alto Isoso (AVIGUZI) y Protección del Guajukaka (guanaco) en Charagua Iyambae*") declaring an area of 2,500 Km^2 as a municipal reserve for guanacos. The latter will encourage further efforts for the protection of the species.

Second, our results also supported the prediction that WPE is causing a contraction of potential suitable habitat for the Chacoan guanacos. We observed a contraction in the area previously occupied by the species (Miserendino *et al.* 1998; Weber 2000) which could be the beginning of a distributional shift and potential loss of the guanaco's geographic range due to habitat replacement, as has been suggested for past geographic distributions of the species in Argentina (Tonni and Politis 1980; Barberena *et al.* 2009). The most obvious explanation for this contraction is the intensive development of a cattle ranch in the area (Angulo and Rumiz 2009). In addition, given the general strong association between guanacos and their preferred open habitats (Travaini *et al.* 2007), together with the reduction by 90 % of grasslands due to WPE (Pinto and Cuéllar-Soto 2017), could be engendering a setback for the long-term survival of the guanaco population under study. There are cases where long-term changes in the structure and composition of grasslands have bolstered declines of small mammal communities (Emmons 2009; Bilney *et al.* 2010; Pardiñas *et al.* 2012; Pardiñas and Teta 2013).

Even though we are concerned by the multiple factors, such as cattle ranching, change in fire regime (severity and frequency), and soil erosion, driving woody plant encroachment (Morello and Adamoli 1974; Devine *et al.* 2017), we urge for a particular focus on conservation efforts in countering consequences of WPE (Midgley and Bond 2001; Moncrieff *et al.* 2009; Kgope *et al.* 2010; Cipriotti and Aguiar 2012). Therefore, we appeal to researchers and decision makers to look beyond the more obvious human-induced pressures on the species (including hunting, competition with domestic livestock and habitat loss or fragmentation resulting from agricultural development; Cunazza *et al.* 1995) and consider the importance of WPE as a direct driver for habitat loss (Wigley *et al.* 2010).

Furthermore, we encourage managers of the 2,500 km^2 reserve, recently created by the Indigenous Autonomous Government of the Bolivian district of Charagua, to adapt their management interventions and conservation strategies, and take into consideration this silent but pernicious process of "thicketisation" of savannahs and grasslands. Finally, we encourage and promote the development of additional studies on this phenomenon given that it could constitute an imminent threat to the region's biodiversity (Archer *et al.* 2017).

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Distributional patterns of the Brazilian free-tailed bat *Tadarida brasiliensis* in the Peruvian territory

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The molossid bat *Tadarida brasiliensis* has a wide and apparently continuous distribution in South America. Although it has been reported in several localities of both versants of the Peruvian Andes, the potential distribution for this species has not been formally analyzed. Therefore, we describe its distributional pattern in the territory and provide comments about the possible influence of the Andes in its distribution. We gathered occurrence records from museums, acoustic surveys, literature, GBIF and Vertnet sources, and we selected localities to minimize spatial correlation. After defining a minimum-convex polygon of Peruvian records as background area, we use Maxent software with bioclimatic variables to construct species distribution models. Several models were evaluated using different metrics, and the model with the lowest AICc was selected. Then, the model was projected for Peruvian territory. *Tadarida brasiliensis* is reported for the first time in Cajamarca, Piura and Ica departments. The potential distribution model showed two disjunct suitable areas, one for the Pacific versant and other for the Amazonian versant of the Andes, but connected with moderate suitable conditions in the Huancabamba Depression region in northern Perú. Mean diurnal range and annual mean temperature were identified as the main limiting factors for the potential distribution of this species in this territory. *Tadarida brasiliensis* exhibits a discontinuous distribution in the Peruvian territory. In northern part, the Huancabamba depression zone has climatic conditions that may allow the east-west dispersal for this species. In central and southern parts, the higher crest of the Andes (> 4,500 m) has low suitable conditions due to the extreme climate. In the eastern, the lowland Amazonian forests has low suitability for this species, probably due to high temperatures. We suggest that the Andes could be acting a biogeographical barrier that limits the dispersal for this species, but population-genetic studies are needed to confirm this hypothesis. We identified that temperature is the main climatic factor that limit the dispersal of this bat. In conclusion, *T. brasiliensis* is mainly associated with desert and Andean slopes ecosystems in Perú, and we highlight the importance of incorporating acoustic records in the analysis of its distribution patterns.

El murciélago molósido *Tadarida brasiliensis* tiene una distribución amplia y aparentemente continua en América del Sur. Si bien se ha reportado en varias localidades de ambas vertientes de los Andes peruanos, la distribución potencial de esta especie no ha sido analizada formalmente. Por lo tanto, describimos el patrón de distribución de *T. brasiliensis* en el territorio peruano y brindamos comentarios sobre la posible influencia de los Andes en su distribución. Recopilamos registros de ocurrencia de museos, estudios acústicos, literatura, GBIF y Vertnet, y seleccionamos localidades para minimizar la correlación espacial. Después de definir un polígono mínimo convexo en base a los registros peruanos como área de calibración, usamos el software Maxent con variables bioclimáticas para construir modelos de distribución de especies. Se evaluaron varios modelos utilizando diferentes métricas y se seleccionó el modelo con el AICc más bajo. Luego, se proyectó este modelo en el territorio peruano. *Tadarida brasiliensis* es reportada por primera vez en los departamentos de Cajamarca, Piura e Ica. El modelo de distribución potencial mostró dos áreas adecuadas disjuntas, una para la vertiente del Pacífico y otra para la vertiente amazónica de los Andes, pero conectadas por las condiciones idóneas de la región de la Depresión de Huancabamba en el norte de Perú. El intervalo medio de temperatura diurna y la temperatura media anual fueron identificadas como los principales factores limitantes para la distribución potencial de esta especie en este territorio. *Tadarida brasiliensis* exhibe una distribución discontinua en el territorio peruano. En la parte norte, la zona de depresión de Huancabamba tiene condiciones climáticas que pueden permitir la dispersión este-oeste de esta especie. En las parte central y sur, los picos más altos de los Andes (> 4,500 m) tiene bajas condiciones adecuadas debido al clima extremo. En el este, los bosques amazónicos de las tierras bajas tienen baja idoneidad para esta especie, probablemente debido a las altas temperaturas. Sugerimos que los Andes podrían estar actuando como una barrera biogeográfica que limita la dispersión de esta especie, pero se necesitan estudios genéticos-poblacionales para confirmar esta hipótesis. Identificamos que la temperatura es el principal factor climático que limita la dispersión de este murciélago. En conclusión, *T. brasiliensis* se asocia principalmente con ecosistemas desérticos y de laderas andinas en el Perú, y destacamos la importancia de incorporar registros acústicos en el análisis de sus patrones de distribución.

Keywords: Andes; geographic barrier; maxent; potential distribution; suitability.

Introduction

The Brazilian free-tailed bat *Tadarida brasiliensis* is a small-size insectivorous bat with one of the widest distributions in the western hemisphere (Wilkins 1989). It occurs in an extensive variety of habitats, ranging from deserts to montane humid forest (Eger 2007), with the ability to forage from the ground up to 3,000 m (McCracken *et al.* 2008). In South America, only the subspecies *T. b. brasiliensis* is recognized (Schwartz 1955). Based on individuals from the east versant of the Andes and the subantarctic sub-region, Morales *et al.* (2018) suggest it apparently conforms to one genetic group. The potential distribution of the species showed it is strongly associated to the Andes (Escobar *et al.* 2015; Romero 2018), with few records in much of Amazonia

(Eger 2007), and presumably absent in lowland forest ecosystems (Wilkins 1989).

In the Peru, this species has been reported in the Equatorial dry forest, the coastal desert, the steppe, the Yungas and the lowland forests ecoregions (Pacheco *et al.* 2009). Due to the variety of occurrence records (Acha and Zapatel 1957; Solari *et al.* 2001; Zeballos *et al.* 2001; Mena and Williams 2002; Zelada *et al.* 2014; Aragón and Aguirre 2014), it is believed that this species presents a continuous distribution in this country (Eger 2007; Barquez 2018). However, the Andean Cordillera, is recognized as a great biogeographical barrier that limits the dispersal of many mammalian species, particularly in bats, between the Pacific and Amazonian versants and could drastically affect *T. brasiliensis* perceived distribution in the country (Koopman 1978; Patterson *et al.* 2012). To date, no analysis of the influence of the Andes, or how environmental conditions, influence the distribution patterns of *T. brasiliensis* in Perú has been conducted.

Species distribution models (SDMs) are frequently used for assessing the potential distribution of species (Razgour *et al.* 2016), based on occurrence records and the environmental characteristics of these localities (Franklin 2010). The main assumption of the models is that the climate of these localities represents part of the environmental component of the species' niche (Peterson and Soberón 2012), and therefore, it is possible to predict suitable areas for species presence. Determining most suitable areas could help us better understand possible geographical and environmental barriers for the species' distributions, and also provide information on its likely dispersal limitations (Barve *et al.* 2011).

The aim of this study is to describe the distribution patterns of *T. brasiliensis* in Perú using species distribution models and explore the possible influence of the Andes. Here, we test the hypothesis that *T. brasiliensis* has a continuous distribution in Perú, including the Andes mountain chain. Additionally, we report novel records in the territory and highlight priority research locations for this species.

Materials and Methods

Occurrence data. Occurrence data were selected from 139 records gathered from the following sources: the collection of mammals, Museo de Historia Natural de San Marcos (MUSM; $n = 51$) in Lima, bat acoustic surveys (this work, $n = 26$), literature (Acha and Zapatel 1957; Zeballos *et al.* 2001; Pari *et al.* 2015; Morales *et al.* 2018; Portugal 2018; $n = 30$), the Global Biodiversity Information Facility (GBIF 2019; download on July 8, 2019; $n = 11$), and Vertnet (Constable *et al*. 2010; download on August 7, 2019; $n = 22$). In order to avoid sampling bias caused by spatial correlation (Razgour *et al.* 2016), localities used as occurrence data were manually chosen such that no two localities were separated less than 25 km, which is the approximate mean displacement of *T. brasiliensis* for foraging flights from their roost (Allen *et al.* 2009). For GBIF and Vertnet sources, only records from scientific collections were considered to avoid spatial bias in the distribution (Beck *et al.* 2014). The majority of the occurrence records (74 %) were dated after 1960. All records covered a temporal range from 1900 to 2019. See selected locality details in Appendix 1.

The acoustic surveys were performed in 23 localities distributed across eight departments of Perú: Ayacucho, Cajamarca, Ica, La Libertad, Lima, Piura, Puno and Tacna, from 2014 to 2019. Recordings were obtained by performing active monitoring in acoustic transects, using Pettersson ultrasonic detectors D240x and M500-384 plugged into digital recorders or mobile phone devices. Recording sessions were performed between 18:00 and 23:00 hrs, in rainless conditions, for one night per site (Kingston 2016). We selected pulses in which the search phase consists of a downward quasi-constant frequency component ranging from 30 kHz to 26 kHz, described as characteristic for this species (Gillam and McCracken 2007; Arias-Aguilar *et al.* 2018). The sound files are stored in the MUSM for further studies involving the development of an acoustic library for Perú.

Novel localities are reported using the political departments of Perú. For the biogeographical analyzes, we used the terrestrial ecoregions of the world (Olson *et al.* 2001) and the biogeographic regionalization of the Neotropical region (Morrone 2014).

Study area. Two types of geographical spaces were delimited: the background and the projection areas. The background area must offer a good coverage of the conditions within the species environmental tolerance (Anderson 2013), and at regional scales, using a specific area to model partial-niche produce more sensitive models (Razgour *et al.* 2016). Thus, we calculated a minimum-convex polygon based on our occurrence data (Brown 2014) and applied a buffer of 50 km. As projection area, we used the layer of the Peruvian territory obtained from Instituto Geográfico Nacional (IGN, www.idep.gob.pe), assuming that it represents an accessible area for this species (Barve *et al.* 2011) and considering that climatic conditions within this area were well represented by the background area (Anderson and Raza 2010). All the geospatial operations were done using ArcMap 10.5.1 (Esri 2016).

Environmental data. Bioclimatic data from the global interpolated climate database WorldClim 1.4 were used (Hijmans *et al.* 2005) with a grid resolution of 30 arc-seconds (~1 km). We downloaded 15 variables representing current climate, but removed Bio 8, Bio 9, Bio 18 and Bio 19 because they can have spatial abnormalities (Escobar *et al.* 2014). We masked these climatic rasters to the extent of the background area to generate background point. To avoid multicollinearity (Elith *et al.* 2011), a Spearman's correlation test between variables were performed using the R package fuzzySim 3.0, to select variables with correlation values lower than 0.85 (Syfert *et al.* 2013). Also, we selected variables considering their relevance to the representative Peruvian climate (Schwarb *et al.* 2011), as well as their relationships with the occurrence of *T. brasiliensis* (Duff and Morrell 2007; Hristov *et al.* 2010).

Distribution model. We constructed an SDM using the maximum entropy algorithm Maxent 3.4.1 (Phillips *et al.* 2018). The background area was used to calibrate the model, and then projected to the Peruvian territory. For calibration, different models were built with 10,000 random background points and evaluated with spatial cross validation. We explored different complexity settings for Maxent: regularization multipliers in intervals of 0.5, ranging from 1.0 to 5.0, and feature class combinations L, Q, H, LQ, LH, QH, LQH, LQHP, and LQHPT, where "L" is linear, "P" is product, "Q" is quadratic, "H" is hinge and "T" stands for threshold (Radosavljevic and Anderson 2014). We performed the evaluation process with the spatial cross validation procedure "checkerboard2" (aggregation factor = 4) using the R package ENMeval 0.3.0 (Muscarella *et al.* 2014) with R 3.5.3 (R Core Team 2019). We evaluated variable importance with Maxent´s variable jackknife test (Phillips *et al.* 2006). Following Warren and Seifert (2011), the model selection was made based on the Akaike information criteria corrected for small samples (AICc) that provide a comparison of the most informative and parsimonious model (Razgour *et al.* 2016). We use the metrics of the model with lowest AICc value and projected it using the Maxent cloglog transformation. Model evaluation details can be found in Appendix 2 and model response curves in Appendix 3.

Results

We found that *T. brasiliensis* is found from sea level (MUSM 4,793, 5,368; Lima department) to 4105 m (ROM 93863, 93868; Junín department) in Perú. In the Pacific versant, the species was found up to 3,149 m (via ultrasonic record), whereas on the Amazonian versant most records are in the Andean piedmont (>1047 m), and only two records are reported in the lowland eastern humid forest of Perú at 360 m (MUSM 6045 194441; San Martín department). With acoustic surveys, we reported for the first time its presence in Cajamarca, Piura and Ica departments. We recognized the occurrence of *T. brasiliensis* in the Desert and the Puna provinces of the South America transition zone, in the Ecuadorian province of the Pacific Dominion, and in the Yungas, the Ucayali and the Rondônia provinces of the South Brazilian dominion.

We selected five variables as most ecologically relevant and not highly correlated (Table 1). Then, from 81 computed models using these variables, we chose the model with the lowest AICc obtained with following parameters: LQ as features class combination and 1 as regularization multiplier (AUCtrain: 0.7836, AUCtest: 0.7211, OR10: 0.0912, AICc: 1073.82, ΔAICc: 0). Based on the evaluation results (Appendix 2 and 4), we observed that in models with more parameters, the average AUCtest increase, which means that these models are stricter than the others. But we also observed that AUCdiff and the OR10 increase with more complexity, what is typically related to overfitting in these more complex models. Our selected model presents less complexity but also the less overfitting in comparison with other models.

Table 1. Selected variables contribution. Selected bioclimatic variables and their contribution in the selected model.

	Variables Contribution	
Potential Distribution Model	**Percent contribution**	**Permutation importance**
Mean Diurnal Range (Bio 2)	57.4731	64.8406
Annual Mean Temperature (Bio 1)	18.4447	28.2832
Temperature Annual Range (Bio 7)	6.6362	6.8761
Precipitation Seasonality (Bio 15)	3.3811	0.000
Annual Precipitation (Bio 12)	14. 0648	0.000

Bioclimatic variables with the greatest influence in the distribution of *T. brasiliensis* were mean diurnal range of temperature (Bio 02) and annual mean temperature (Bio 01), which contribute to 64.8 % and 28.3 % to the model, respectively. Response curves of each variable (Appendix 3) showed that annual temperatures between 15 to 20°C present predicted values over 0.5, while temperatures over 10°C in mean diurnal ranges reduce significantly the predicted values of occurrence. The jackknife test showed that the variable with the highest gain when used in isolation was annual mean temperature, while the one which decreased the gain the most when omitted was mean diurnal temperature.

The SDM showed a slightly disjunct distribution for *T. brasiliensis* in Perú, where two different core areas with high suitability values (> 0.5) were obtained (Figure 1). The first area corresponded to the coastline ecosystems in the Pacific versant of the Andes, included in the Desert and Xeric Shrublands biome, where higher predictive values seem to be restricted to the Sechura desert and Tumbes-Piura dry forest ecoregions. The other area corresponded to Andean slopes ecosystems in the Amazonian versant, where higher predictive values were detected above 1000 m, in the Yungas and wet Puna ecoregions. In northern Perú, a moderately suitable area in the Huancabamba Depression region, connects the western and eastern suitable areas. The higher part of the Andes (above 4500 m elevation) exhibited low environmental suitability (< 0.2) for this species. Similarly, the lower Amazonian forest had low environmental suitability (< 0.4).

Discussion

It was previously reported that *T. brasiliensis* has a broad and continuous distribution in Perú (Wilkins 1989; Eger 2007; Barquez *et al.* 2015); however, based on our model, we reject that hypothesis. Our correlative model predicted that this species has a largely discontinuous distribution in the country, where two disjunct areas with high suitability values could be identified: the Pacific and Amazonian versants, separated by the Andes. Contrary to the model presented by Escobar *et al.* (2015), we identified highly suitable environmental conditions in the coastal and Andean slopes ecosystems. Furthermore, supporting Wilkins (1989), we found this species is mostly absent in lowland forest of the Amazonia.

Based on the localities of occurrence and the predictions of the model, we identified two areas in the Peruvian territory that have not been sampled enough or remain unassessed for this species: the Huancabamba depression zone and the eastern slopes of the central Peruvian Andes. In the Huancabamba depression zone, although the SDM showed moderate suitability (0.4 to 0.6), no specimens are known to occur in this zone or in the vicinity (less than 25 km). Thus, we consider that the Huancabamba depression zone remains poorly studied and requires increased focus on bat research priorities. On the other hand, the eastern slopes of the central Peruvian Andes –specially the zone between Junín and Pasco departments– where our model indicated moderate suitability (~ 0.6) is one the better surveyed areas in the country (Mena 2010; Arias *et al.* 2016). We believe that *T. brasiliensis* has yet to be detected in this geographic area, because most surveys have only used mist nests, a methodology with only moderate efficiency when in collecting insectivorous bats (Rydell *et al.* 2002).

Despite the information gaps, we consider that our model efficiently represents the environmental niche of this species in Perú, in great part because our occurrence data covered a great part of the territory. We accomplished this, by incorporating ultrasonic records which increased data occurrence in about 41 % (Appendix 1); therefore, we support recent suggestions that acoustic surveys contribute and complement traditional methodologies in studying insectivorous bat species (Hintze *et al.* 2019).

Our model estimated only a moderate suitability index (~ 0.6) in the dry forests of the Huancabamba depression. Although this zone was proposed as an important biogeographical barrier for montane species (Weigend 2004), this region was also suggested as an east-west corridor that allow gene flow in *Sturnira erythromos* and likely other species (Pacheco and Patterson 1992). We currently lack occurrence data for *T. brasiliensis* in this region, but considering the low elevation of the Andean in this area (Pacheco 2002), we propose that the species likely uses the depression to connect populations on the eastern versant with those of the western versant of the Andes. Future biological inventories in the area will test this hypothesis.

On the other hand, in central and southern Perú, our model revealed broad separation in the suitable environmental conditions for the potential distribution of the species. Due to the topographic characteristics and the extreme climate conditions in the higher elevations (Garreaud 2009), the Andes are considered as important biogeographical barrier for several groups of mammals (Patterson *et al.* 2012). However, the role of the Andes as a biogeographic barrier for bats has seen little debate since the pioneering works of Koopman (1978) and Pacheco and Patterson (1992), but it has been argued that only few bat species are capable of inhabiting high elevations (Patterson *et al.* 1998). Although *T. brasiliensis* has the ability to fly up to 3,000 m above the ground to forage (McCracken *et al.* 2008), our model suggest that this species is limited by extreme climatic conditions on the highest parts of the central and southern Andes, likely due to cold weather and permanent snow (Garreaud 2009). Additionally, we believe that biological factors could also influence its distribution in the higher elevations of the Andes (Krauel *et al.* 2018). For example, the diet of *T. brasiliensis* includes coleopterans, lepidopterans, hemipterans and dipterans (Lee and McCracken 2002; Alurralde and Díaz 2018), but the diversity and abundance of these insects declines with increasing elevation (Hodkinson 2005). Therefore, reduced prey availability could make it difficult for this species to inhabit the higher Andes.

Furthermore, our model also revealed high suitable conditions restricted to the deserts and Lomas ecosystems of the Pacific versant (Figure 1). As in other western bat species in Perú, such as *Artibeus fraterculus* (Patterson *et al.* 1992) and *Glossophaga soricina* (Webster 1993), the homogeneous climatic conditions of this ecoregion (Rundel *et al.* 1991) could have allowed the latitudinal dispersal of *T. brasiliensis* close to the coastline (Wiens and Donoghue 2004). However, the biogeographical processes by which this species arrived to these ecoregions are still

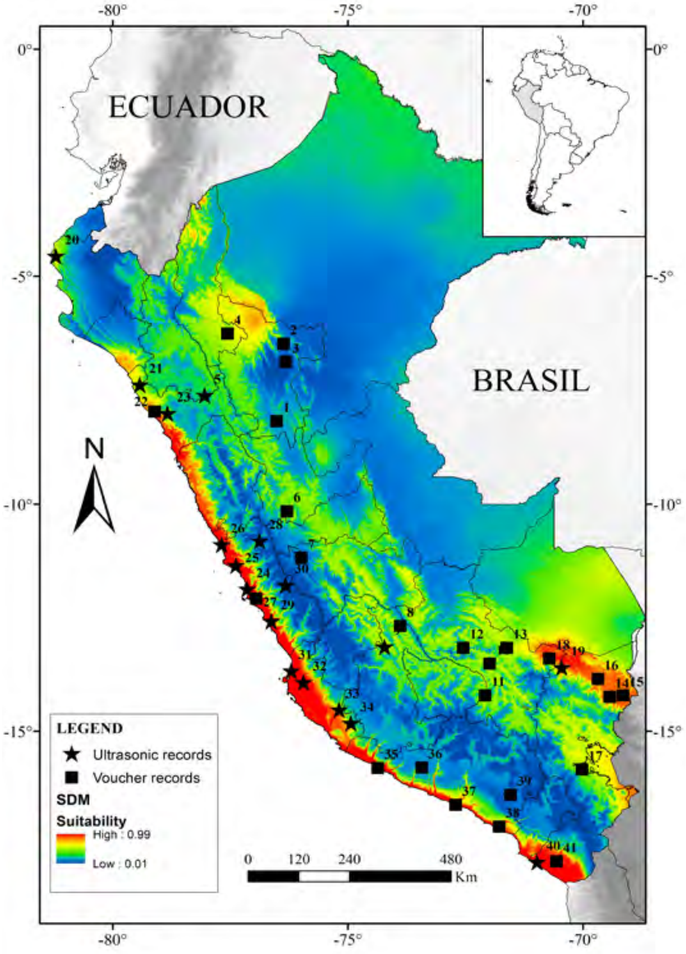

Figure 1. Selected localities and the potential distribution model (SDM) of *T. brasiliensis* in the Peruvian territory.

unknown (Lim 2009). We believe that the Huancabamba depression is closely related to the distributional patterns in South America, but population-level phylogenetic studies of the individuals from the central Andean mountains and Pacific versant are needed to test dispersal hypothesis.

Based on our model, it could be expected that individuals from the eastern and western versant have accumulated some degree of genetic variation. Genetic differentiation between individuals from different versants has been reported for other Neotropical bats, resulting in some cases in the validation or description of new species, such as *Lophostoma occidentalis* (Velazco and Cadenillas 2011), *Sturnira bakeri* (Velazco and Patterson 2014), and *Artibeus aequatorialis* (Larsen *et al.* 2010). In North America, studies on intraspecific genetic variation for *T. brasiliensis* suggested that genetic structure is correlated with niche differentiation (Morales *et al.* 2016) and not with the currently recognized subspecies boundaries (Russell and McCracken 2005; Morales *et al.* 2016). Morales *et al.* (2018) found that individuals of *T. brasiliensis* from South America formed a unique population group based on the combined analysis of molecular and morphometric data; however, their study did not include representative data for populations from the Pacific versant of Perú or Ecuador. Thus, we highlight that a genetic survey for *T. brasiliensis* considering samples from both versants is badly needed.

In the Amazonian versant, our model reveals that lowland humid forests ecosystems present few suitable areas for the species (Figure 1). Although the distribution map of Wilkins (1989) seems to include a small part of Amazonia with this ecosystem, and Pacheco *et al.* (2009) stated the species was present in the lowland forest ecoregion (*sensu* Brack-Egg 1986), we found only two records in lowland forests (San Martin Department). In the apparent absence of east geographical barriers for bats in Perú (Proches 2006) and considering the ability of this bat to fly long distances (McCracken *et al.* 2008), the limitation of dispersal for *T. brasiliensis* in this ecosystem is probably related with climate conditions and/or biotic interactions (Peterson and Soberón 2012). The climate in lowland Amazonian forests is characterized by high precipitation and temperature (Vieira *et al.* 2004), with remarkable seasonal variation in the southeast (Jenkins 2009). Since our models revealed that the potential distribution of *T. brasiliensis* is highly influenced by mean diurnal range and annual mean temperature, and considering that ambient temperatures affect metabolic rates in bats (Reichard *et al.* 2010), it is likely that high temperatures in this ecosystem are one of the most important limiting factors for the species. Although it was documented that *T. brasiliensis* prefers temperatures between 22 to 32 °C to develop optimally (Herreid 1967), response curves of our model showed that suitable values of temperature vary between 15 to 20 °C in the Perú; higher temperatures may generate hyperthermia in this bat, limiting its dispersal and supporting what we stated.

Additionally, in the Amazonian forests, there are other possible limiting factors. The high plant diversity (Cardoso *et al.* 2017) and dense coverage that characterize the lowland tropical forest (Nogueira *et al.* 2005; Nabe-Nielsen 2001) could limit the open-space flight of insectivorous bats such as *T. brasiliensis* (Fenton 1990; Kalko 1997). In addition, it is reported that this species usually roosts in caves or human dwellings (Allen *et al.* 2009), which are scarce in this type of forest (García-Rosell 1965; Kvist and Nebel 2000); thus, potential roosting sites may represent another factor that restricts the niche of *T. brasiliensis* in this territory.

In general, our model suggests *T. brasiliensis* is mainly associated with deserts and Andean slopes ecosystems (Figure 1). Further, a great number of locality records in South America and previous work on potential distributions support this pattern (Escobar *et al.* 2015). However, due to the difficulties in capturing *T. brasiliensis* with conventional methods (Rydell *et al.* 2002), we highlight the importance of incorporating acoustic records proceeding from reliable sources to increase the number of records and therefore to improve modelling precision, especially when certain Andean and Amazonian regions remain poorly studied. Notably, the ecological mechanisms associated with geographical dispersal in South America and potential speciation in widespread species, such as *T. brasiliensis*, has yet to be completely investigated (Pyron and Burbrink 2009).

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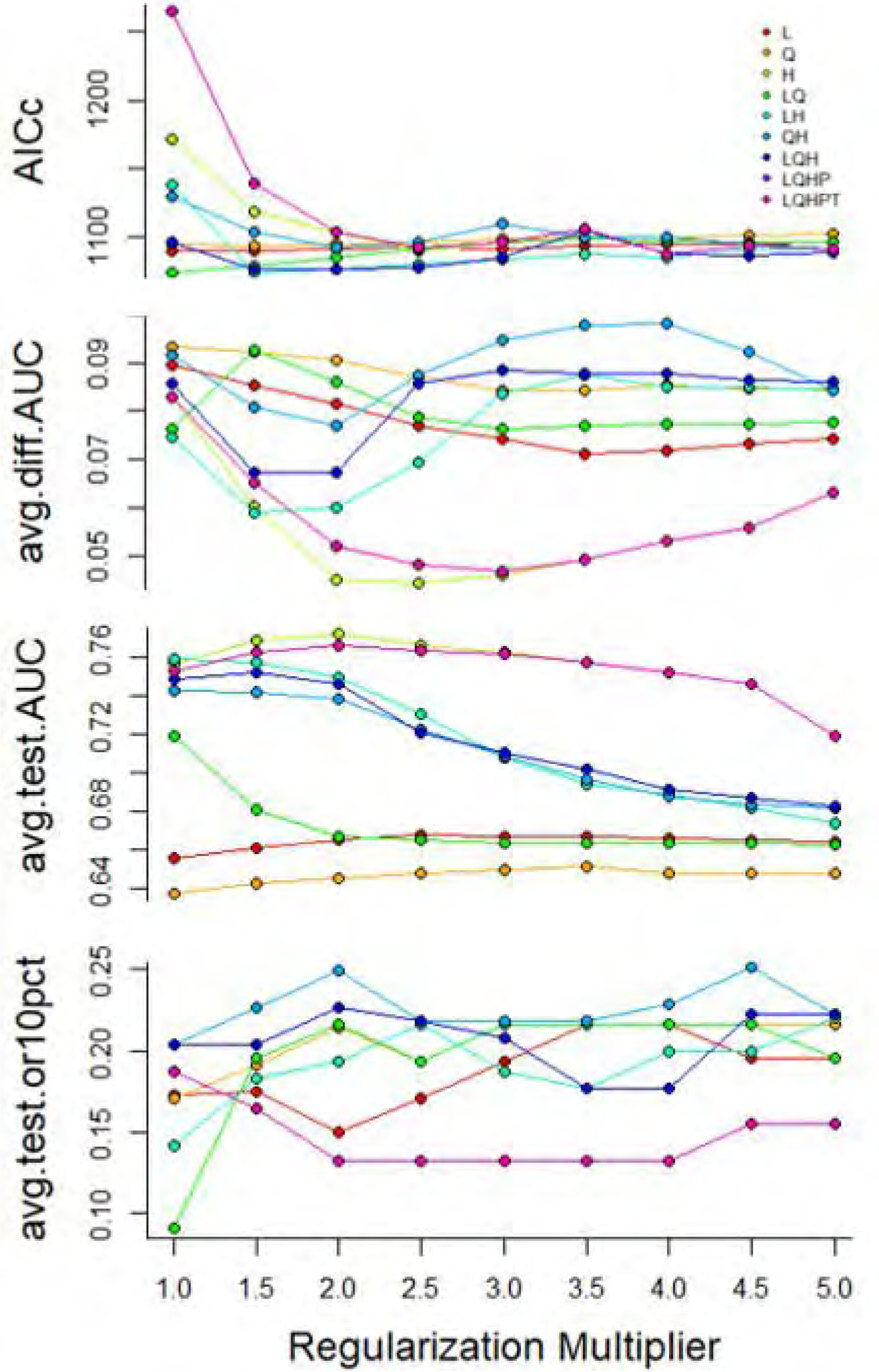
Appendix 1

Selected localities used for the SDM of *T. brasiliensis* in the Peruvian territory. Occurrence records were taken from the following institutions: Museo de Historia Natural de San Marcos (MUSM); Field Museum of Natural History (FMNH); Royal Ontario Museum (ROM); National Museum of Natural History (NMNH); American Museum of Natural History (AMNH). Records with an asterisk (*) are specimens examined by Morales *et al.* (2018). Acoustic records were obtained between 2014 to 2019 and remain stored in MUSM.

N°	Departament	Locality	Terestial ecoregions	Bliogeographics Provinces	Coordinates		Year	Type of record
1	San Martín	Tocache, Qa San Francisco	Ucayali Moist Forest	Ucayali province	-08° 11′ 21.3″ S	-76° 30′ 51.4″ W	1948	MUSM 6045
2	San Martín	Tarapoto	Ucayali Moist Forest	Ucayali province	-06° 28′ 59.9″ S	-76° 22′ 00.0″ W	1954	Acha and Zapatel (1957)
3	San Martín	Río Ponasa	Ucayali Moist Forest	Ucayali province	-06° 53′ 06.0″ S	-76° 19′ 00.9″ W	1954	Acha and Zapatel (1957)
4	Amazonas	Molinopampa	Peruvian Yungas	Ucayali province	-06° 15′ 34.7″ S	-77° 33′ 30.9″ W	2011	MUSM 37049
5	Cajamarca	Cajabamba	Peruvian Yungas	Puna province	-07° 37′ 20.6″ S	-78° 02′ 49.5″ W	2019	Ultrasonic call
6	Huánuco	Huacar	Peruvian Yungas	Yunga province	-10° 09′ 24.9″ S	-76° 17′ 34.6″ W	1982	MUSM 5114-5119
7	Junín	Junín city	Central Andean Wet Puna	Puna province	-11° 10′ 39.5″ S	-75° 59′ 21.6″ W	NA	ROM 93863, 93868*
8	Ayacucho	La Mar	Peruvian Yungas	Yunga province	-12° 41′ 00.0″ S	-73° 52′ 59.9″ W	1941	GBIF (FMNH 52909)
9	Ayacucho	San Cristobal de Huamanga	Peruvian Yungas	Yunga province	-13° 08′ 54.0″ S	-74° 13′ 18.3″ W	2019	Ultrasonic call
10	Cuzco	Santa Ana	Central Andean Wet Puna	Yunga province	-13° 30′ 41.2″ S	-71° 58′ 59.5″ W	NA	NMNH 194443*
11	Cuzco	Chumbivilcas	Peruvian Yungas	Yunga province	-14° 12′ 42.4″ S	-72° 04′ 48.8″ W	2009	MUSM 25965
12	Cuzco	Machu Picchu	Peruvian Yungas	Yunga province	-13° 09′ 47.0″ S	-72° 32′ 44.0″ W	NA	NMNH 194440*
13	Cuzco	Paucartambo	Peruvian Yungas	Rondônia province	-13° 09′ 43.9″ S	-71° 37′ 10.9″ W	2001	MUSM 19421, 19422
14	Puno	Sandia	Peruvian Yungas	Rondônia province	-14° 14′ 41.9″ S	-69° 25′ 51.9″ W	1900	AMNH 16074*
15	Puno	Sandia	Bolivian Yungas	Rondônia province	-14° 12′ 34.9″ S	-69° 08′ 56.0″ W	2009	MUSM 26758
16	Puno	Carabaya	Peruvian Yungas	Rondônia province	-13° 51′ 00.0″ S	-69° 41′ 00.0″ W	1941	GBIF (FMNH 52968)
17	Puno	Carabaya	Central Andean Wet Puna	Yunga province	-15° 50′ 21.6″ S	-70° 01′ 09.8″ W	1941	FMNH 52675*
18	Puno	Carabaya	Peruvian Yungas	Rondônia province	-13° 23′ 59.9″ S	-70° 43′ 00.0″ W	1950	Vertnet (FMNH 68548)
19	Puno	Interoceánica	Peruvian Yungas	Rondônia province	-13° 36′ 11.8″ S	-70° 27′ 10.5″ W	2018	Ultrasonic call
20	Piura	Talara	Tumbes-Piura Dry Forest	Ecuadorian province	-04° 33′ 27.9″ S	-81° 12′ 39.3″ W	2017	Ultrasonic call
21	La Libertad	Cañoncillo	Sechura Desert	Desert province	-07° 23′ 24.1″ S	-79° 25′ 24.8″ W	2018	Ultrasonic call
22	La Libertad	Loma Cerro Campana	Sechura Desert	Desert province	-07° 58′ 30.0″ S	-79° 06′ 30.0″ W	2013	Zelada *et al.* (2014)
23	La Libertad	Menochuco	Sechura Desert	Desert province	-08° 01′ 25.5″ S	-78° 50′ 16.4″ W	2018	Ultrasonic call
24	Lima	Humedales Ventanilla	Sechura Desert	Desert province	-11° 52′ 37.5″ S	-77° 08′ 41.4″ W	2017	Ultrasonic call
25	Lima	Lomas de Lachay	Sechura Desert	Desert province	-11° 21′ 27.9″ S	-77° 23′ 00.5″ W	2017	Ultrasonic call
26	Lima	Albuferas Medio Mundo	Sechura Desert	Desert province	-10° 53′ 51.6″ S	-77° 41′ 12.1″ W	2014	Ultrasonic call
27	Lima	La Molina	Sechura Desert	Puna province	-12° 04′ 50.1″ S	-76° 56′ 52.0″ W	2017	MUSM 47378
28	Lima	Churín	Sechura Desert	Desert province	-10° 48′ 53.3″ S	-76° 52′ 35.8″ W	2019	Ultrasonic call
29	Lima	Azpitia	Sechura Desert	Desert province	-12° 35′ 11.7″ S	-76° 37′ 57.4″ W	2017	Ultrasonic call
30	Lima	San Mateo	Central Andean Wet Puna	Desert province	-11° 47′ 11.3″ S	-76° 19′ 39.0″ W	2019	Ultrasonic call
31	Ica	Humedales de Caucato	Sechura Desert	Desert province	-13° 40′ 32.9″ S	-76° 12′ 16.7″ W	2019	Ultrasonic call
32	Ica	Villacuri	Sechura Desert	Desert province	-13° 55′ 48.5″ S	-75° 56′ 44.4″ W	2019	Ultrasonic call
33	Ica	Plaza Palpa	Sechura Desert	Desert province	-14° 32′ 01.1″ S	-75° 11′ 06.5″ W	2019	Ultrasonic call
34	Ica	Plaza Nazca	Sechura Desert	Desert province	-14° 49′ 39.7″ S	-74° 56′ 13.4″ W	2019	Ultrasonic call
35	Arequipa	Atiquipa	Sechura Desert	Desert province	-15° 48′ 30.0″ S	-74° 21′ 46.0″ W	NA	Zeballos *et al.* (2001)
36	Arequipa	Caravelí	Sechura Desert	Desert province	-15° 47′ 50.3″ S	-73° 25′ 42.8″ W	NA	Pari *et al.* (2015)
37	Arequipa	Cueva Camaná	Sechura Desert	Desert province	-16° 37′ 25.0″ S	-72° 42′ 33.0″ W	NA	Pari *et al.* (2015)
38	Arequipa	Valle de Tambo	Sechura Desert	Desert province	-17° 06′ 09.9″ S	-71° 46′ 55.8″ W	NA	Zeballos *et al.* (2001)
39	Arequipa	Arequipa city	Sechura Desert	Desert province	-16° 23′ 55.9″ S	-71° 32′ 13.1″ W	NA	Pari *et al.* (2015)
40	Tacna	Humedales de Ite	Sechura Desert	Desert province	-17° 53′ 13.8″ S	-70° 58′ 43.7″ W	2014	Ultrasonic call
41	Tacna	Valle de Sama	Sechura Desert	Desert province	-17° 51′ 54.0″ S	-70° 33′ 43.0″ W	2015	Portugal (2018)

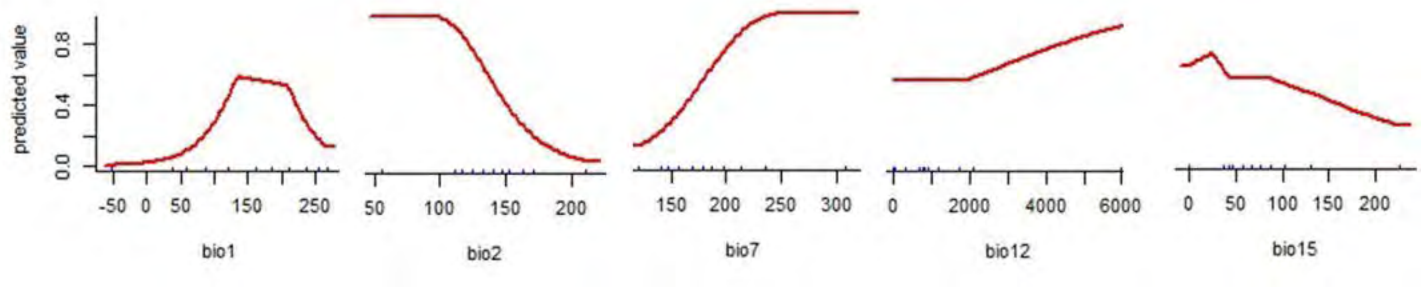
Appendix 2

Model evaluation details. The selection of the model was made using: delta AICc, average AUCdiff, omission rate at 10th percentile presence threshold, and average AUCtest. Evaluations were made with the "checkerboard2" spatial partition schema. The feature class combinations were: L: linear, P: product, Q: quadratic, H: hinge and T: threshold. The evaluation process was performed using ENMeval package version 0.3.0 (Muscarella *et al.* 2014).



Appendix 3

Response curves. Response curves obtained by the selected model for each selected variable are reported.



Appendix 4

Results of evaluation of the parameters. Results of evaluation of parameters performed in the R package ENMeval 0.3.0, considering the selected variables.

Features	Rm	train.AUC	avg.test.AUC	avg.diff.AUC	avg.test.orMTP	avg.test.or10pct	AICc	delta.AICc	Parameters
L	1	0.6785	0.6545	0.0901	0.0833	0.1727	1089.4835	15.6557	5
Q	1	0.6691	0.6344	0.0955	0.0833	0.1705	1092.1535	18.3257	4
H	1	0.8319	0.7642	0.0762	0.0477	0.1642	1171.2578	97.4301	24
LQ	1	0.7836	0.7211	0.0762	0.0686	0.0913	1073.8277	0.0000	6
LH	1	0.8208	0.7552	0.0785	0.0477	0.1831	1137.3702	63.5424	21
QH	1	0.8244	0.7419	0.0925	0.0477	0.2684	1100.4562	26.6285	16
LQH	1	0.8221	0.7472	0.0870	0.0477	0.2456	1095.2968	21.4690	15
LQHP	1	0.8265	0.7567	0.0792	0.0477	0.1642	1218.7652	144.9375	27
LQHPT	1	0.8265	0.7567	0.0792	0.0477	0.1642	1218.7652	144.9375	27
L	1.5	0.6785	0.6599	0.0867	0.0833	0.1746	1090.1189	16.2911	5
Q	1.5	0.6714	0.6403	0.0938	0.0833	0.1913	1093.0100	19.1823	4
H	1.5	0.8163	0.7747	0.0507	0.0477	0.1850	1112.6823	38.8545	16
LQ	1.5	0.7668	0.6805	0.0943	0.1083	0.1955	1078.2007	4.3729	6
LH	1.5	0.8011	0.7531	0.0628	0.0477	0.1831	1075.1797	1.3519	8
QH	1.5	0.8065	0.7405	0.0810	0.0477	0.2267	1109.3867	35.5590	16
LQH	1.5	0.8044	0.7474	0.0715	0.0477	0.2248	1081.0063	7.1785	10
LQHP	1.5	0.8066	0.7635	0.0562	0.0477	0.1623	1124.3387	50.5109	18
LQHPT	1.5	0.8066	0.7635	0.0562	0.0477	0.1623	1124.3387	50.5109	18
L	2	0.6772	0.6643	0.0841	0.0833	0.1496	1091.0507	17.2229	5
Q	2	0.6736	0.6441	0.0921	0.0833	0.2140	1094.3039	20.4761	4
H	2	0.8107	0.7690	0.0439	0.0477	0.1538	1104.7173	30.8896	14
LQ	2	0.7411	0.6667	0.0894	0.1083	0.2390	1083.7044	9.8766	6
LH	2	0.7937	0.7383	0.0657	0.0477	0.2248	1074.9997	1.1720	7
QH	2	0.8016	0.7287	0.0849	0.0477	0.2182	1113.2738	39.4460	16
LQH	2	0.7974	0.7321	0.0775	0.0477	0.2494	1077.9907	4.1630	8
LQHP	2	0.8039	0.7630	0.0492	0.0477	0.1538	1114.9026	41.0749	16
LQHPT	2	0.8039	0.7630	0.0492	0.0477	0.1538	1114.9026	41.0749	16
L	2.5	0.6765	0.6672	0.0808	0.0833	0.1496	1092.2950	18.4672	5
Q	2.5	0.6758	0.6470	0.0891	0.0833	0.1932	1096.0801	22.2524	4
H	2.5	0.8041	0.7611	0.0475	0.0477	0.1538	1090.4313	16.6035	10
LQ	2.5	0.7119	0.6645	0.0821	0.0833	0.1932	1090.2051	16.3773	6
LH	2.5	0.7858	0.7180	0.0761	0.0250	0.2078	1085.1064	11.2787	9
QH	2.5	0.7959	0.7111	0.0946	0.0477	0.2182	1097.7182	23.8905	12
LQH	2.5	0.7897	0.7070	0.0940	0.0477	0.2182	1081.8063	7.9786	8
LQHP	2.5	0.8056	0.7600	0.0487	0.0477	0.1538	1094.0688	20.2411	11
LQHPT	2.5	0.8056	0.7600	0.0487	0.0477	0.1538	1094.0688	20.2411	11
L	3	0.6759	0.6675	0.0772	0.1042	0.1705	1091.2385	17.4107	4
Q	3	0.6773	0.6495	0.0854	0.0852	0.2159	1098.4081	24.5803	4
H	3	0.8021	0.7564	0.0496	0.0477	0.1538	1085.9274	12.0996	8
LQ	3	0.6755	0.6633	0.0781	0.1269	0.2159	1097.6606	23.8329	6
LH	3	0.7798	0.6979	0.0819	0.0250	0.1557	1082.0946	8.2669	7
QH	3	0.7883	0.6982	0.0975	0.0705	0.2182	1101.6644	27.8366	12

Apendix 4 continuación...

Features	Rm	train.AUC	avg.test.AUC	avg.diff.AUC	avg.test.orMTP	avg.test.or10pct	AICc	delta.AICc	Parameters
LQH	3	0.7827	0.6983	0.0927	0.1102	0.1557	1093.0987	19.2710	10
LQHP	3	0.8021	0.7556	0.0501	0.0477	0.1538	1085.9274	12.0996	8
LQHPT	3	0.8021	0.7556	0.0501	0.0477	0.1538	1085.9274	12.0996	8
L	3.5	0.6759	0.6677	0.0723	0.1061	0.2159	1092.8782	19.0504	4
Q	3.5	0.6758	0.6509	0.0852	0.0625	0.2159	1098.6055	24.7777	3
H	3.5	0.8009	0.7513	0.0528	0.0477	0.1538	1091.6724	17.8446	9
LQ	3.5	0.6721	0.6640	0.0776	0.1061	0.1951	1097.7642	23.9365	5
LH	3.5	0.7718	0.6887	0.0797	0.1102	0.1992	1085.6237	11.7960	7
QH	3.5	0.7784	0.6924	0.0958	0.0705	0.1869	1130.5313	56.7036	17
LQH	3.5	0.7705	0.6904	0.0871	0.1102	0.1557	1097.9921	24.1644	10
LQHP	3.5	0.8009	0.7513	0.0528	0.0477	0.1538	1091.6724	17.8446	9
LQHPT	3.5	0.8009	0.7513	0.0528	0.0477	0.1538	1091.6724	17.8446	9
L	4	0.6736	0.6672	0.0725	0.0852	0.1951	1094.8511	21.0233	4
Q	4	0.6723	0.6487	0.0856	0.0625	0.2159	1101.4590	27.6312	3
H	4	0.7985	0.7408	0.0585	0.0477	0.1765	1101.8029	27.9752	11
LQ	4	0.6708	0.6640	0.0776	0.1269	0.1951	1096.9411	23.1134	4
LH	4	0.7516	0.6836	0.0797	0.1102	0.1765	1092.7787	18.9509	8
QH	4	0.7643	0.6843	0.0921	0.0790	0.1850	1113.4687	39.6410	13
LQH	4	0.7538	0.6852	0.0803	0.1330	0.1992	1091.2361	17.4084	7
LQHP	4	0.7985	0.7408	0.0585	0.0477	0.1765	1101.8029	27.9752	11
LQHPT	4	0.7985	0.7408	0.0585	0.0477	0.1765	1101.8029	27.9752	11
L	4.5	0.6701	0.6665	0.0734	0.0852	0.1951	1097.2066	23.3789	4
Q	4.5	0.6713	0.6486	0.0851	0.0625	0.2159	1100.4614	26.6336	2
H	4.5	0.7951	0.7263	0.0631	0.0477	0.1557	1101.3407	27.5129	10
LQ	4.5	0.6702	0.6642	0.0775	0.1269	0.2159	1095.4363	21.6086	3
LH	4.5	0.7222	0.6761	0.0820	0.1102	0.1992	1088.3320	14.5043	5
QH	4.5	0.7442	0.6787	0.0858	0.0790	0.1680	1098.5480	24.7202	8
LQH	4.5	0.7345	0.6792	0.0805	0.1102	0.1765	1087.7865	13.9588	5
LQHP	4.5	0.7951	0.7263	0.0631	0.0477	0.1557	1101.3407	27.5129	10
LQHPT	4.5	0.7951	0.7263	0.0631	0.0477	0.1557	1101.3407	27.5129	10
L	5	0.6692	0.6655	0.0745	0.0852	0.1951	1095.8348	22.0071	3
Q	5	0.6723	0.6488	0.0852	0.0625	0.2159	1101.5643	27.7365	2
H	5	0.7895	0.7060	0.0723	0.0477	0.1557	1101.9515	28.1238	9
LQ	5	0.6696	0.6639	0.0781	0.1061	0.2159	1096.4307	22.6029	3
LH	5	0.7099	0.6704	0.0833	0.1102	0.2201	1089.9782	16.1505	5
QH	5	0.7254	0.6729	0.0791	0.0477	0.1680	1095.2162	21.3884	6
LQH	5	0.7196	0.6725	0.0825	0.1102	0.1992	1089.9919	16.1642	5
LQHP	5	0.7895	0.7060	0.0723	0.0477	0.1557	1101.9515	28.1238	9
LQHPT	5	0.7895	0.7060	0.0723	0.0477	0.1557	1101.9515	28.1238	9

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A new bat species of the genus *Myotis* with comments on the phylogenetic placement of *M. keaysi* and *M. pilosatibialis*

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Molecular studies of Neotropical *Myotis* (Chiroptera, Vespertilionidae) in the last decade have uncovered substantial cryptic diversity. One example is *M. keaysi pilosatibialis*, which is characterized by a complex taxonomy derived from low morphological variation. Herein, we studied cryptic diversity of a high elevation clade from premontane and montane forest of Chiriquí Province (Panamá), Cordillera Oriental (Ecuador), and Valle del Silencio (Costa Rica). Additionally, we disentangle relationships of *M. k. keaysi* and *M. k. pilosatibialis* by determining their phylogenetic placement within the Neotropical *Myotis* radiation. In the process, we identified a new lineage of species level hierarchy that is described herein. We used an integrative taxonomy approach, using a combination of linear morphometrics, qualitative morphology, molecular phylogenetics, and climatic analysis. The newly identified lineage is a sister species to *M. pilosatibialis str.,* but differs from *M.* sp. (Quintana Roo, México), *M. keaysi str.*, and *M. oxyotus gardneri* in size and other quantitative morphological characters in addition to both nuclear and mitochondrial DNA sequence divergence. Based on our phylogenetic analysis of partial cytochrome *b* sequence, the polyphyly of *M. keaysi str.* and *M. pilosatibialis str.* is resolved, with *M. keaysi str.* paraphyletic to *M. ruber* and *M. simus*. *Myotis pilosatibialis* is part of a monophyletic clade that is sister to the newly identified species. This report refines our understanding of taxonomy and systematics of the *Myotis pilosatibialis* complex of bats, identifies and describes a new species of *Myotis,* and more broadly it contributes to efforts to characterize species in this genus in Neotropical environments. Based on its distribution, we classified this newly described species as paramontane due to its restriction to premontane and montane forest of Chiriquí Province (Panamá), Valle del Silencio (Costa Rica), and Cordillera Oriental (Ecuador). These habitats are susceptible to the effects of climate change, in addition to ongoing habitat destruction.

Los estudios de genética molecular del género de murciélagos Neotropicales *Myotis* (Chiroptera: Vespertilionidae) han permitido descubrir diversidad críptica en la última década. Un ejemplo es *M. keaysi pilosatibialis*, el cual se caracteriza por una taxonomía compleja con poca variabilidad morfológica. En esta investigación, estudiamos un clado de murciélagos myotinos de los bosques premontanos y montanos de la Provincia de Chiriquí (Panamá), Cordillera Oriental (Ecuador) y el Valle del Silencio (Costa Rica). Adicionalmente, resolvemos las relaciones de *M. k. keaysi* y *M. k. pilosatibialis* al determinar su posición filogenética en la radiación de *Myotis* en el Neotrópico. En el proceso, identificamos una entidad biológica a nivel de especies que es descrita es esta contribución. Desde un enfoque de taxonomía integrativa, utilizamos una combinación de morfometría lineal, caracteres morfológicos cualitativos, así como análisis filogenéticos moleculares y de clima. La nueva especie es evolutivamente cercana a *M. pilosatibialis str,* pero difiere de *M.* sp. (Quintan Roo, México), *M. keaysi str.* y *M. oxyotus gardneri* por su tamaño y otros caracteres morfológicos cuantitativos, así como divergencia evolutiva en secuencias de genes mitocondriales y nucleares. Con base a nuestro análisis filogenético del fragmento parcial del gen citocromo *b*, resolvemos las relaciones polifiléticas de *M. keaysi str.* y *M. pilosatibialis str.* *Myotis keaysi str.* es parafilético en relación con *M. ruber* y *M. simus*. *M. pilosatibialis str.* forma parte de un clado monofilético hermano a este nuevo linaje. Este trabajo contribuye a refinar la taxonomía y sistemática del complejo de especies *Myotis pilosatibialis*, identifica y describe una especie nueva de *Myotis*, así como aporta de una manera más amplia a los esfuerzos de caracterizar especies de este género en ambientes neotropicales. Basado en su distribución geográfica, este nuevo clado de murciélagos myotinos se clasifica como paramontano, debido a su distribución a bosques premontanos y montanos de los Chiriquí (Panamá), Valle del Silencio (Costa Rica) y Cordillera Oriental (Ecuador). Estos hábitats son susceptibles a los efectos del cambio climático y la continua destrucción del mismo.

Keywords: Armien's *Myotis*; Chiriquí province; Cordillera Oriental; cryptic diversity; *Myotis armiensis*; Neotropics; Valle del Silencio.

Introduction

Bats of the widely distributed genus *Myotis* are an excellent model for studies of diversification and historical biogeography (Stadelmann *et al.* 2007; Ruedi *et al.* 2013). With *ca.* 134 species (www.mammaldiversity.org), *Myotis* is one of the more remarkable mammalian radiations worldwide. Although long considered to be a classic example of an adaptive radiation in temperate regions, more detailed studies of Neotropical (Larsen *et al.* 2012a, b) and Afrotropical species (Patterson *et al.* 2019) using molecular data are now uncovering substantial cryptic diversity (Bickford *et al.* 2007) in tropical regions.

Based on previous systematic revisions (La Val 1973; Hernandez-Meza *et al.* 2005; Wilson 2008; Moratelli and Wilson 2014; Mantilla-Meluck and Muñoz-Garay 2014), the nominal species *M. keaysi* was partitioned into two subspecies: *M. k. keaysi* J. A. Allen 1914, distributed in the Andes of Colombia, Colombian Caribbean, Perú, Ecuador, Bolivia, and Argentina above 1,100 m, with most specimens known from above 2,000 m and *M. k. pilosatibialis* (La Val 1973), occurring in northern Venezuela, the island of Trinidad, Colombian Caribbean, eastern cordillera of the Colombian Andes, and elsewhere from southern México, southeastward through Central America into northwestern Panamá. Both subspecies are known to occur in sympatry in Caribbean Colombia and the eastern cordillera of Colombia. Although the phylogenetic placement for both is still pending, Mantilla-Meluck and Muñoz-Garay (2014) recognized *pilosatibialis* as distinct at the species level based on morphology. Based on those findings, Moratelli and Wilson (2014) recommended reassigning the specimens previously assigned to *M. keaysi* by Stadelmann *et al.* (2007) and Ruedi *et al.* (2013) from Yucatán (México) to *M. pilosatibialis*. Furthermore, Moratelli *et al.* (2016) and Moratelli *et al.* (2017) were unable to confidently identify these specimens from Yucatán, México and assigned provisionally a "cf ." (Latin, confer), preceding the specific epithet.

Myotis keaysi as envisioned by Stadelmann *et al.* 2007 and Ruedi *et al.* 2013 was identified as a monophyletic clade with considerable geographic structure and at least three different lineages (Larsen *et al.* 2012a; Chaverri *et al.* 2016), which were named as follows: *M. keaysi* (Yucatán Peninsula, México), *M.* cf. *keaysi* 2 (México, El Salvador, Guatemala), and an unnamed clade from the mountain tops of Cordillera Oriental from Ecuador and Panamá (Clare *et al.* 2011; Larsen *et al.* 2012b) that was later suggested to be *M. keaysi* (Costa Rica) in Chaverri et al. (2016).

In this study, we provided the phylogenetic placement for *M. keaysi str.* and *M. pilosatibialis str.* in the *Myotis* Neotropical radiation and under this phylogenetic framework, we reviewed specimens from the unnamed clade from mountain tops of Chiriquí (Panamá) and Cordillera Oriental (Ecuador). We found that these specimens are distinct from other species of Neotropical *Myotis* and described this new species based on the General Lineage Concept (GLC), which uses the concept of species as separately evolving metapopulation lineages that can be recognized using diverse secondary recognition criteria (De Queiroz 2007). We apply the criteria used by Florio *et al.* (2012) as follows: a) identify lineages based on clades from analysis of multiple molecular markers b) employ multivariate procedures such as principal component analysis (PCA) and discriminant function analysis (DFA) to determine morphological variation associated with these phylogenetic groups, and c) use climatic analysis to evaluate the environment and geographic space occupied by the groups supported by covariation of genetic and morphological evidence.

Methods

Specimens in Panamá were collected under an ongoing project entitled "Caracterización de la epidemiología y ecología de enfermedades zoonóticas trasmitidas por vectores (emergentes y reemergentes) en áreas silenciosas y conocidas de Panamá" signed by Instituto Conmemorativo Gorgas and Ministerio del Medio Ambiente de Panamá, with permits SC/A-50-1 and SEX/A-1-19. In Ecuador, specimens were collected under the project "Caracterización de la diversidad biológica y genética de los mamíferos del Ecuador", signed by Pontificia Universidad Católica del Ecuador and Ministerio del Medio Ambiente (MAE), with permits (MAE-DNB-CM-2016-004 and 70-12-2017- DPAN/MAE). Specimens in both countries were collected with ground-level mist netting and field methods generally followed Galbreath *et al.* (2019), under guidelines of the American Society of Mammalogists (Sikes *et al.* 2016) and approved by the University of New Mexico Animal Care and Use Committee.

Specimens examined. Specimens directly examined ($n = 72$) for this research include representatives of Central and South American *Myotis*, including type specimens (Appendix I). These comprise fluid-preserved specimens, stuffed skins, and skulls deposited in the following institutions: American Museum of Natural History (AMNH); Field Museum of Natural History, Chicago (FMNH); Natural History Museum, University of Kansas (KU); Natural History Museum of Los Angeles County, Los Angeles (LACM); Louisiana State University Museum of Natural Science (LSUMZ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museum of Southwestern Biology, University of New Mexico (MSB); National Museum of Natural History, Smithsonian Institution (USNM); Museo de Zoología, División de Mastozoología, Pontificia Universidad Católica del Ecuador (QCAZ); Royal Ontario Museum (ROM); Sam Noble Oklahoma Museum of Natural History, University of Oklahoma (SNOMNH); Texas A&M Biodiversity Research and Teaching Collection, College Station (TCWC); Museum of Texas Tech University (TTU; Dunnum *et al.* 2018). These specimens were identified according to Wilson (2008), Moratelli and Wilson (2011), Moratelli *et al.* (2013), Moratelli *et al.* (2017).

Measurements. All measurements are in millimeters (mm) or grams (body mass) and are from adults. The lengths of head and body (HB), tail, hind foot, ear, and the body weight (mass) were recorded from skin labels and are reported to the nearest millimeter or nearest gram. Forearm length (FA) and third metacarpal length (3ML) were directly measured from specimens. Measurements were taken using digital calipers accurate to 0.02 mm. Craniometric measurements were taken under a binocular microscope at low magnification (usually 6x). These dimensions were recorded and analyzed to the nearest 0.01 mm, but values were rounded off to 0.1 mm throughout the text because this is the smallest unit allowing accurate repeatability with calipers (Voss *et al.* 2013).

Measurements include four external, 14 cranial, and two mandibular dimensions. The measurements and abbreviations are defined as follows: forearm length (FA), from the elbow to the distal end of the forearm including carpals; third metacarpal length (3ML), from the distal end of the forearm including carpals to the distal end of the third metacarpal; length of dorsal hairs (LDH), from the base to the tip of the hair in the fur between the scapulae; length of ventral hairs (LVH) in fur at mid thorax; greatest length of the skull (GLS), from the apex of the upper internal incisors to the occiput; condylocanine length (CCL), from the anterior surface of the upper canines to a line connecting the occipital condyles; condylobasal length (CBL), from the premaxillae to a line connecting the occipital condyles; incisive length (CIL), from the apex of upper internal incisors to a line connecting the occipital condyles; basal length (BAL), from the apex of upper internal incisors to the ventral margin of the foramen magnum; zygomatic breadth (ZB), greatest breadth across the outer margins of the zygomatic arches; mastoid breadth (MAB) greatest breadth across the mastoid region (MAB); braincase breadth (BCB), greatest breadth of the globular part of the braincase; interorbital breadth (IOB), least breadth between the orbits; postorbital breadth (POB), least breadth across frontal posterior to the postorbital bulges; breadth across canines (BAC), greatest breadth across outer edges of the crowns of upper canines, including cingulae; breadth across molars (BAM), greatest breadth across outer edges of the crowns of upper molars; maxillary toothrow length (MTL), from the upper canine to M3; molariform toothrow length (M1-3), from M1 to M3; mandibular length (MAL), from the mandibular symphysis to the condyloid process; and mandibular toothrow length (MAN), from the lower canine to m3. Measurements and abbreviations are further defined in Moratelli *et al.* (2013). Descriptive statistics (mean and range) were calculated for all dimensions. The cranial index (CRI= (((IOB + BCB) x GLS)/2)) and a modification of the maxillary index (MXI = (((BAC + BAM) x MTL)/2)) were as used by Baud and Menu (1993) and López-González *et al.* (2001). We used capitalized colors from (Ridgway 1912).

Principal component analysis (PCA) and discriminant function analysis (DFA) were used to examine overall patterns of skull size and shape variation among samples. We selected the following cranial dimensions representing different axes of length and width of the skull, rostrum and mandible: GLS, CCL, CBL, CIL, BAL, MAB, BCB, IOB, POB, BAC, BAM, MTL, M1-3, MAL, MAN. To obtain a more balanced design for multivariate analysis, we selected a minimum of 4 and maximum of 10 adult specimens, totaling 33 individuals (17 females and 16 males). Males and females were pooled together to enhance analysis. PCA was used to summarize trends in size and shape variation (total data set was considered a unique sample). We conducted a varimax rotation of the loading matrix after PCA in order to have more interpretable factors with a simpler structure that can be obtained using orthogonal rotations. We used rotated PCA scores to test for statistical significance of difference among species. This was assessed by multiple analysis of variance MANOVA, with Pillai's Trace. This previous analysis was followed by one-way ANOVA. A post-hoc multiple comparison Bonferroni corrected approach was used to evaluate pairwise differences among species (Rice1989).

DFA was used to assess craniometric characters that best discriminate samples, with a priori identification of samples (Moratelli *et al.* 2013). For DFA, probabilities for misclassification rates were also assessed and individuals were resigned using a jackknife procedure. Missing data values were estimated using Amelia R package (0 % of total data set) from raw data set (Honaker *et al.* 2011). We checked for normality assumptions and measurements were log transformed (Zar 1998). Finally, variance-covariance matrices were computed using all variables.

Statistical analyses were performed in software R (R Core Team 2020). We used the following R packages as follows: MASS (DFA analysis), stats (PCA analysis), ggplot2 and ggord (graphics and visualization), factoextra (eigenvalues extraction), psych (varimax rotation), car (MANOVA analysis), rstatix (summary statistics, T-test, ANOVA, adjust P-values for multiple comparisons, formatting and adding significant symbols; Venables and Venables and Ripley 2002; Wickham 2016; Beck 2017; Fox and Weisberg 2019; Revelle 2020; Kassambara 2020; Kassambara and Mundt 2020.

We contrasted the skull size and shape of *M.* sp. n. (*n* = 10) from Chiriquí (Panamá) and Cordillera Oriental (Tungurahua Province, Ecuador); *M. pilosatibialis str.*, including the holotype specimen (*n* = 8); *M. keaysi str.* from Puno and Cuzco, Perú (*n* = 5); *M. oxyotus. gardneri*, including the holotype specimen (*n* = 6) from Costa Rica and Panamá; and specimens provisionally labelled as *M.* cf. *pilosatibialis* (*n* = 4) from Quintana Roo, Yucatán Peninsula, México, hereafter called *M.* sp. We included *M. pilosatibialis str.* (El Salvador, Guatemala, Honduras and México) and *M.* sp. (Quintana Roo, Yucatán, México) due to its close morphological similarity and phylogenetic proximity (Larsen *et al.* 2012a; Moratelli *et al.* 2016; Moratelli *et al.* 2017). Similarly, we included specimens that morphologically match *M. oxyotus gardneri* La Val 1973, which was recorded in syntopy with the newly identified lineage at Chiriquí Province (Panamá) and Valle del Silencio (Costa Rica). Likewise, we included *M. keaysi str.* from Perú, due to resemblance in external dimensions, cranial morphology and fur traits. Qualitative traits employed here to characterize and distinguish species follow Moratelli *et al.* (2013). Capitalized color nomenclature follows Ridgway (1912).

DNA Extraction, Sequencing, Editing, and Assembly of partial cytochrome b and nuclear genes. To obtain DNA sequence data, whole DNA was extracted from liver, muscle or wing tissues, following a guanidinium isothiocyanate extraction protocol, E.Z.N.A. Tissue DNA Kit (Omega), and DNeasy Blood & Tissue Kit (Qiagen). Samples were quantified using Nanodrop® ND-1000 (NanoDrop Technologies, Inc) or Qubit fluorometer kit (Invitrogen), resuspended and diluted to 25 ng/ul in ddH$_2$O prior to amplification.

We relied on different primers and PCR protocols, which are reported as follows: cytochrome *b* in Hoffmann and Baker

(2001); Larsen *et al.* (2012b); and Naidu *et al.* (2012); nuclear exon and intron genes in Matthee and Davis (2001); Eick *et al.* (2005); Larsen *et al.* (2012b); Lack *et al.* (2010); Roehrs *et al.* (2010); and Salicini *et al.* (2011). We targeted ~ 710 bp of cytochrome-*b* sequence (*n* = 11), 1, 038 bp of nuclear exon, (RAG2) recombination activating gene II sequence (*n* = 13), and intron region of other 3 genes, 402 bp of protein kinase C, iota sequence (PRKCI, *n* = 14), 414 bp signal transducer and activator of transcription 5A sequence (STAT5A, *n* = 14), and 475 bp of thyrotropin sequence (THY, *n* = 14). Sequencing was conducted using Applied Biosystems 3110 Sequencer of the molecular biology facility at the University of New Mexico (UNM). In Ecuador, successful amplified PCR products were sent for sequencing to the commercial laboratory Macrogen Inc in Seoul, South Korea. Editing and assembly of sequences were performed with Geneious Prime (BioMatters Ltd. 2020).

DNA Extraction and Sequencing of cytochrome oxidase c subunit I. We retrieved partial sequences of cytochrome *c* oxidase subunit I (657 bp) from mitochondrial genomes for the following species: *M. oxyotus gardneri* (*n* = 1), *M. pilosatibialis str.* (*n* = 2), *M.* sp. (*n* = 1, Quintana Roo, Yucatán, México), and *M.* sp. n. (*n* = 2). DNA was extracted using standard manual extraction methods such as DNeasy Blood & Tissue Kit (QUIAGEN, Hilden, Germany) following manufacturers guidelines, as well as one open method based on magnetic particle using KingFisher™ Duo (Thermo Fisher Scientific). DNA was incorporated into double stranded DNA short fragment libraries built following BEST protocol (Mak *et al.* 2017; Carøe *et al.* 2018) using BGISEQ-500 adapters. Libraries were sequenced using 100 base paired end read chemistry on a BGISEQ-500 sequencer machine (BGI-Copenhagen).

Mitogenomes assembly and annotation. Low quality base reads, missing bases and adapters were trimmed followed by adapters removal using Adapter Removal v2 (Lindgreen 2012; Schubert *et al.* 2016). We built mitochondrial genomes using NOVOPlasty (Dierckxsens *et al.* 2017) using as reference the mitochondrial genome of *Myotis lucifugus* accession number (NC_029849.1). Furthermore, annotation was carried on with MitoZ (Meng *et al.* 2019).

DNA Alignments and *Phylogenetic analysis.* Alignments of sequences were performed with Geneious Prime (BioMatters Ltd. 2020), using MUSCLE (Edgar 2004). Phylogenetic analysis of mitochondrial and nuclear sequences was conducted with newly generated sequences and sequences retrieved from GenBank for Neotropical species of *Myotis* previously known to form a monophyletic clade (Ruedi *et al.* 2013). We included previously generated sequences from GenBank for cytochrome-*b* for 91 individuals (Ruedi and Mayer 2001; Kawai *et al.* 2003; Rodriguez and Ammerman 2004; Stadelmann *et al.* 2004; Kawai *et al.* 2006; Stadelmann *et al.* 2007; Baird *et al.* 2008; Larsen *et al.* 2012a, b; Patterson *et al.* 2019), including unpublished data by Parlos *et al.* (2008); COXI for 51 individuals used in Chaverri *et al.* (2016); RAG2 for 14 individuals; PRKCI for 13 individuals; STAT5A for 13 individuals; and THY for 14 individuals (Lack *et al.* 2010; Roehrs *et al.* 2010)

Outgroup selection. For cytochrome *b* phylogeny, we selected three sequences of *M. gracilis*, one sequence of *M. brandtii* and one sequence of *M. yanbarensis*, which are sister species to Neotropical *Myotis*. For our cytochrome *c* oxidase subunit I phylogeny, four sequences of *M. brandtii*, and one sequence of *M. lucifugus* were used. In our species tree analysis, we included myotine bats from the Nearctic clade as well, therefore we selected the eastern Palearctic lineage *M.* cf. *ikonnikovi* as the outgroup.

Maximum likelihood trees were generated using IQ-TREE with 100 bootstraps and 1000 replicates (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016). We used the program ModelFinder (Kalyaanamoorthy *et al.* 2017) with Bayesian information criteria (BIC) for selecting a nucleotide substitution model for cytochrome-*b*, cytochrome oxidase *c* subunit I, exon and intron regions. Heterozygous nuclear introns alleles were statistically resolved using PHASE 2.1.1 (Stephens *et al*. 2001) prior to the inclusion in further analyses. We used SEQPHASE web server (Flot, 2010) to generate the input files for PHASE. The Bayesian analysis was conducted in MrBayes v.3.2 for partial cytochrome *b* and cytochrome *c* oxidase subunit I (Ronquist *et al.* 2012). The search started with a random tree and the Markov chain was run for 10 million generations with trees sampled every 1,000 generations in two replications. Default values were kept for the "*relburning*" and "*burninfrac*" options in MrBayes, therefore the first 25.000, 00 generations were discarded as burn in, and posterior probability estimates of all model parameters were based on the remaining trees. Tree convergence and stationary was accessed in the Bayesian analysis by plotting the likelihood values in Tracer v1.7.1 (Rambaut *et al.* 2018).

We follow Moratelli *et al.* (2017) when designating nodal support in the mitochondrial gene trees; for ML analyses there is a strong support for bootstraps values above ≥ 75 %, moderate support for values > 50 % and < 75 %; and negligible for support for values ≤ 50 %. For the BI analysis, there are two categories, with significant support in cases in which a node posterior probability was ≥ 0.95, and insignificant or negligible support for posterior probability values < 0.95.

Identification of molecular synapomorphies. For the identification of unique molecular synapomorphies for the newly identified lineage, we generated maximum parsimony trees from mitochondrial data sets and intron regions of 3 nuclear genes using PAUP* (Swofford 2003). For these analyses, characters were treated as unordered and equally weighted. We performed a heuristic search with random addition of sequences and tree bisection-reconnection branch swapping. We set maxtree limit to 1000, with the goal of applying a maxtree limit of 100 to each 10 random addition sequence replicate. To measure clade support, 1000 bootstrap replicates were performed on a 50 % majority-rule consensus tree. We used the command *describet-*

rees and *apolist* with delayed transformation (DELTRAN) to obtain a list of molecular synapomorphies. To polarize character state transformation, we used outgroups previously used in maximum likelihood and Bayesian analyses.

Genetic distances. We calculated K2P distances (these were computed for comparisons with previous molecular studies on Neotropical *Myotis*; *e. g*, Larsen *et al.* 2012a, b) expressed as percentages and pairwise genetic distances using uncorrected sequence divergence (*p*-distances), and modeled in MEGAv10.17 (Kumar *et al.* 2016) for mitochondrial genes.

Species tree and species delimitation. Under the multispecies coalescent model, we inferred both species tree and species delimitation. For species tree inference we used *BEAST (Heled and Drummond 2010) method using the software suite available in BEAST 2.6.2 (Bouckaert *et al.* 2019). We used three phased intron and one exon alignments with substitution, clock, and tree models unlinked among all loci. All loci were assigned the log-normal relaxed-clock model using a Yule prior and linear with constant root population size model. We decided not to include mtDNA, due to its potentially strong influence on species tree inference given its higher variability and that assumptions of lower ploidy are not always met (which is modelled by *BEAST; McLean *et al.* 2016). We ran the analysis for 1 x 10^8 generations in two replicates, saving the results every 10,000 generations. The first 10 % of each run was discarded as burn-in and assembled using LOGCOMBINER v.1.10.4 to produce a maximum clade credibility tree in TREEANNOTATOR v1.10.4. Likewise, we used Tracer v.1.7.1 to access convergence and stationarity of model parameters based on ESS values and examination of tree files.

We used STACEY v1.2.1 (Species Tree and Estimation classification, Yarely), implemented in BEAST 2.6.2 (Jones 2017; Bouckaert *et al.* 2019). This method requires no prior assignment of individual to species, and no guided tree. We ran the analysis for 2 x 10^8 generations in two replicates. After completion, we used Species Delimitation Analyzer (Jones 2015) to process log files and find the distribution over species assignments under two collapse height priors (collapse 0.0001 and 0.0005). Tracer v.1.7.1 was used to assess convergence and stationarity of model parameters based on ESS values and examination of tree files. All newly generated sequences were deposited in GenBank with accession numbers MW025265-MW025275 and MW041968 - MW042028; (see Appendix II for cytochrome *b* sequences, Appendix III for cytochrome *c* oxidase subunit *I* and Appendix IV for nuclear sequences, including previously generated ingroup and outgroup sequences used in this study).

Climatic analysis. Species climatic envelopes have been used for establishing species boundaries in cryptic species (Florio *et al.* 2012). To evaluate climatic differences among species that are closely related to *Myotis* sp. n., we only included specimens used in phylogenetic analysis (*n* = 19). We extracted values for 19 climatic variables in WorldClim at 2.5 arc second resolution (Fick and Hijmans 2017). Prior to conduct PCA analysis, we carried out a Pearson´s correlation analysis to indicate presence of multicollinearity among climatic variables. Based on this analysis, we selected nine bioclimatic variables as follows: BIO1 = Annual Temperature, BIO2 = Mean Diurnal Range, BIO4 = Temperature seasonality, BIO5 = Max Temperature of the Warmest Month, BIO6 = Min Temperature of the Coldest Month seasonality, BIO12 = Annual Precipitation, BIO13 = Precipitation of the Wettest Month, BIO14 = Precipitation of the Driest Month and BIO15 = Precipitation seasonality.

We conducted a principal component analysis to examine the degree of climatic variation among species, then we ran a MANOVA using informative rotated PC´s, followed by a post-hoc multiple comparison approach using a Bonferroni corrected approach, to evaluate pairwise differences among species. Statistical analyses were performed in software R (R Core Team 2020).

Results

Phylogenetic analysis. The partial cytochrome *b* alignment contained 145 sequences with 1, 140 columns, 620 distinct patterns, 434 informative sites, 66 singleton sites and 640 constant sites. ModelFinder found that the Best-fit model was the Hasegawa-Kishono-Yano, with empirical base frequencies allowing for a proportion of invariable sites plus discrete Gamma model (HKY + F + I + G4), whilst our cytochrome *c* oxidase subunit I alignment contained 61 sequences with 657 columns, 216 distinct patterns, 188 informative sites, 22 singleton sites and 447 constant sites. ModelFinder found Hasegawa-Kishono-Yano, with empirical base frequencies plus discrete Gamma model (HKY + F + G4) as the Best-Fit model according to BIC.

Both maximum likelihood and Bayesian phylogenetic analysis of mitochondrial genes sequences (Figures 1 and 2) from specimens that morphologically match *M. pilosatibialis str. sensu* La Val (1973), were recovered as part of a monophyletic clade containing specimens from Guatemala, El Salvador, and México. This clade was found well-supported in cytochrome *b* analyses, with negligible support found in the cytochrome *c* oxidase subunit I phylogenetic tree. A specimen from Guatemala was geographically closest to the type locality in Honduras, therefore, we followed La Val (1973) in referring to this clade as *M. pilosatibialis str*.

In our cytochrome *b* phylogenetic tree, a clade formed by sequences from specimens of *M pilosatibialis str.* is sister to a well-supported high elevation clade formed by specimens from Chiriquí and Cordillera Oriental (Ecuador), hereafter called *M.* sp. n., whilst our cytochrome *c* oxidase subunit I, analysis retrieved a supported clade from Costa Rica, Panamá and Ecuador samples as sister to *M.* sp. (Quintana Roo, Yucatán, México).

The phylogenetic placement of *M.* sp. (Quintana Roo, Yucatán, México) differs in our cytochrome *b* phylogenetic analysis, being paraphyletic to a well-supported monophy-

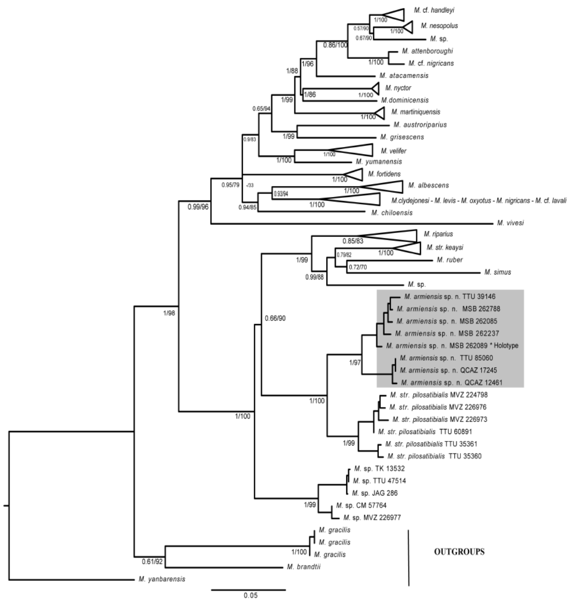

Figure 1. Partial cytochrome *b* phylogeny resulting from bayesian and maximum likelihood inference, with shaded grey sequences of *M. armiensis* sp. n., including holotype. The Bayesian analysis was conducted in MrBayes and maximum likelihood trees were generated using IQ-TREE with 100 bootstraps and 1000 replicates. Scores are bootstrap and probabilities values. Nodal support is shown right and left of slashes (" /") respectively.

letic clade formed by *M.* sp. n. + *M. pilosatibialis str.* and the *ruber* group (*simus, keaysi, ruber, riparius,* sp.). *M*. sp. n. is part of well supported clade in both mitochondrial topologies. Within the *ruber* group, we were able to obtain a cytochrome *b* sequence from a specimen that morphologically matches *M. keaysi sensu* La Val (1973) from Cochabamba, Bolivia which is the specimen geographically nearest to the type locality of Minas at Puno, Perú.

M. sp. n. is genetically distinct using both mitochondrial markers, the genetic pairwise distances between *M*. sp. n. and other species studied range from 6.1 to 12 %, *p*-distance 0.06 – 0.11 in partial cytochrome *b*, and from 3.6 to 9.8 %, *p*-distance 0.03 – 0.08 in partial cytochrome *c* oxidase subunit I. In partial cytochrome *b*, we retrieved the lowest value for conspecific populations from Chiriquí and eastern Cordillera Oriental (Ecuador; 3.1 %, *p*-distance 0.03). For cytochrome oxidase *c* oxidase subunit I, the lowest value was retrieved between conspecific populations from Valle del Silencio (Costa Rica) and Chiriquí Province (Panamá; 0.0 %, p-distance 0.00). Distance values are of the same order of magnitude as other interspecific and intraspecific comparisons within the taxa compared (Table 1).

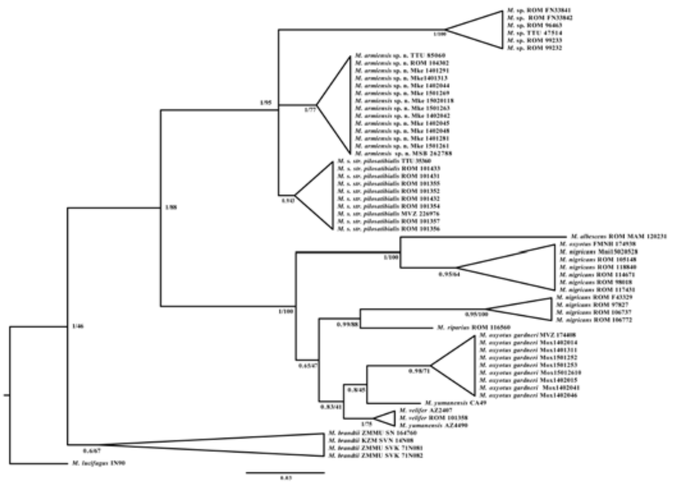

Figure 2. Partial cytochrome oxidase *c* subunit I phylogeny resulting from bayesian inference and maximum likelihood inference. The Bayesian analysis was conducted in MrBayes and maximum likelihood trees were generated using IQ-TREE with 100 bootstraps and 1000 replicates. Scores are bootstrap and probabilities values. Nodal support is shown right and left of slashes (" /") respectively.

Our species tree analysis readily identified *M.* sp. n. as genetically distinct from other species in the Neotropical and Nearctic *Myotis* radiation. Although we recovered relatively low support values for the newly identified clade, this topology also depicts a sister species relationship between conspecific populations from Chiriquí (Panamá) and Cordillera Oriental (Ecuador) as previously shown in our mitochondrial phylogenetic analyses (Figure 3). Results from two STACEY replicates analyses using nuclear data set suggested 20 putative species, under two collapse heights (0.0001 and 0.0005). Among the delimitated species, we found *M.* sp. n. as a candidate to be evaluated under an integrative taxonomy approach using independent data.

Morphological analysis. The principal component analysis comparing all five species extracted two major components that accounted for 53.0 and 30.3 % of the variation (Figure 4; Table 2). The PCA plot shows that *M.* sp. n. overlaps partially with *M. pilosatibialis str.*, which is due to size and shape similarities, while all of the other species were distinct. *M. str. keaysi* and *M. oxyotus gardneri* plotted at the lower left end of PC1 reflecting their larger size, whilst *M*. sp.

Table 1. Matrix of genetic distances (partial cytochrome *b* and cytochrome *c* oxidase subunit I) within and among three species of *Myotis*, where *armiensis* sp. n. in divided in two clades in cytochrome *b* analysis and three clades in cytochrome *c* oxidase subunit I. Below the diagonal:pairwise genetic distance using Kimura 2-parameter model (percentage). On the diagonal within clade distance using the Kimura 2-parameter model (percentage). Above the diagonal:pairwise *p*-distance values. Number of specimens sequenced in parenthesis.

	Partial Cytochrome-b				
Species/clades	**1**	**2**	**3**	**4**	**5**
1 *M. armiensis* sp. n. Panamá (5)	**1.0**	0.03	0.06	0.11	0.09
2 *M. armiensis* sp. n. Cordillera Oriental (Ecuador) (3)	3.1	**0.0**	0.06	0.11	0.09
3 *M. pilosatibialis* (6)	6.2	6.1	**2.0**	0.11	0.11
4 *M. keaysi* (1)	12.0	11.7	11.7	**n.a**	0.11
5 *M.* sp. (5)	9.8	10.1	10.0	12.1	**2.0**
	Partial Cyto-chrome c oxidase subunit I				
Species/clades	**1**	**2**	**3**	**4**	**5**
1 *M. armiensis* sp. n. Panamá (2)	0.0	0.01	0.01	0.03	**0.08**
2 *M. armiensis* sp. n. Cordillera Oriental (Ecuador) (1)	1.8	n.a	0.01	0.03	**0.08**
3 *M. armiensis* sp. n. Costa Rica (11)	0.0	1.8	0.0	0.03	**0.08**
4 *M. pilosatibialis* (6)	3.6	3.8	3.6	0.0	**0.07**
5 *M.* sp. (5)	9.5	8.7	9.8	8.1	**1.3**

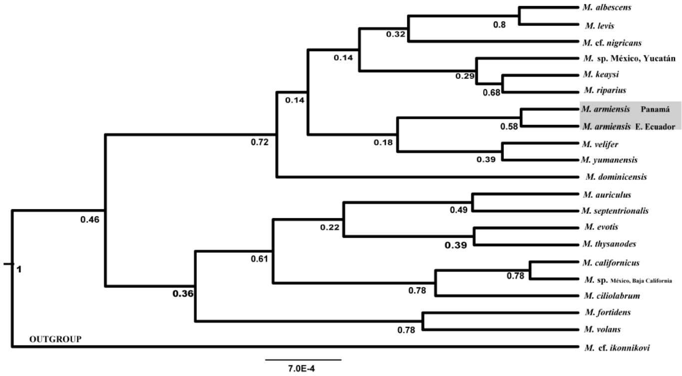

Figure 3. Species tree inferred in *BEAST using multilocus sequence data for New World *Myotis*. Number under branches represent bayesian posterior probability values with conspecific populations from Ecuador and Panama shaded grey.

(Quintana Roo, Yucatán, México) plotted at the right lower end, which is explained by its small size. PC1 shows variation in size and is influenced most by variables related to length of the skull, having MAL, GLS, CCL, CBL, CIL and M1–M3 with loadings above 0.8. PC2 shows shape variation, and it is most influenced by measurements associated with the width of the skull, with BCB and POB having loadings above 0.8.

A one-way multivariate analysis of variance suggested there was a statistically significant difference between all species on both PC1 and PC2, as suggested by Pillai's Trace test, $F_{(8,58)} = 15.411$, $P < 0.001$. Follow-up ANOVAs showed that this dissimilarity occurred at both PC´s (PC1, $F_{(4,29)} = 15.9$, $P < 0.05$, PC2, $F_{(4,29)} = 15.0$, $P < 0.05$). Post-hoc multiple comparison analyses revealed that *M*. sp. n. is different from *M. oxyotus gardneri* ($P < 0.01$), and *M. str. keaysi* ($P < 0.05$) in PC1, and different from *M*. sp.(Quintana Roo, Yucatán, México; $P < 0.001$) and *M. str. pilosatibialis* ($P < 0.05$) in PC2. For other comparison, see Appendix V.

Table 2. Factor loading after PCA and varimax rotation, with Kaiser Normalization for two principal components from a principal component analysis (PCA). The analysis is based on 15 craniometric measurements of five species, including 33 individuals. See Methods for variable abbreviations.

Measurements	PC I	PC II
MAL	-.939	.231
MAN	-.695	.585
GLS	-.914	.318
CCL	-.862	.444
CBL	-.866	.423
CIL	-.944	.245
BAL	-.754	.574
MAB	-.751	.323
BCB	----	.921
IOB	-.645	.564
POB	-.374	.812
BAC	-.337	.599
BAM	-.513	.761
MTL	-.765	.575
M1-M3	-.840	.299
eigenvalues	11.14	1.34
% of variance explained	53.0	30.3
cumulative %	53.0	83.3

Table 3. Vector coefficient correlations between original variables and discriminant functions (DF1 and DF2) for selected samples of *Myotis*.

Measurements	DF1 (83.5%)	DF2 (9.9%)
MAL	-32.71	-179.89
MAN	135.04	62.82
GLS	215.37	-84.56
CCL	-120.75	-83.33
CBL	42.31	-75.27
CIL	-136.83	-52.95
BAL	70.81	-144.96
MAB	190.98	142.86
BCB	21.57	49.32
IOB	.67	-23.05
POB	18.80	-36.78
BAC	-97.68	106.43
BAM	38.63	-76.04
MTL	-89.95	-23.80
M1-M3	78.38	85.67

Although *M*. sp. n. is overlapping partially with *M. pilosatibialis*, our DFA analysis readily distinguishes *M*. sp. n. from other species along the first axis (83.5 %) and to a lesser extent the second axis (9.9 %, Figure 5; Tabla 3). The jackknifed classification matrix showed that the analysis correctly classified 81.8 % of the specimens, with *M*. sp. n. 70 % correctly classified, *M. str. pilosatibialis* 75 % correctly classified, *M*. sp. (Quintana Roo, Yucatán, México) 100 % correctly classified, *M. str. keaysi* 75 % correctly classified, and *M. oxyotus gardneri* 100 % classified.

Cranial index of *M*. sp. n. (CRI: 50.6) is larger than *M. str. pilosatibialis* (CRI: 47.3), *M*. sp. (Quintana, Roo, Yucatán, México, CRI: 42.1), but smaller than *M. str. keaysi* (CRI: 51.5) and *M. oxyotus gardneri* (CRI: 53.8).

Climatic analysis. Our PCA for climatic variables resulted in three PCA´s with eigenvalues > 1, explaining 85.6 % of the total variation. PCA1 was primarily informative for Min Temperature of the Coldest Month, whilst Mean Diurnal range was the principal driver along PCA2. In contrast

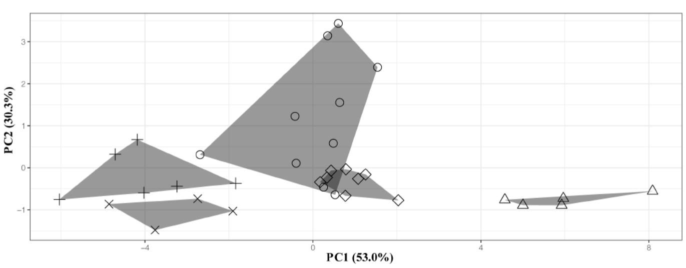

Figure 4. Principal components (PC´s) from a PCA based on 15 cranial measurements from 33 individuals. Samples:*M. armiensis* sp. n (circles), *M*. sp. (triangles), *M. oxyotus gardneri* (+ symbols), *M. keaysi str.* (X symbols), and *M. pilosatibialis str.* (diamonds).

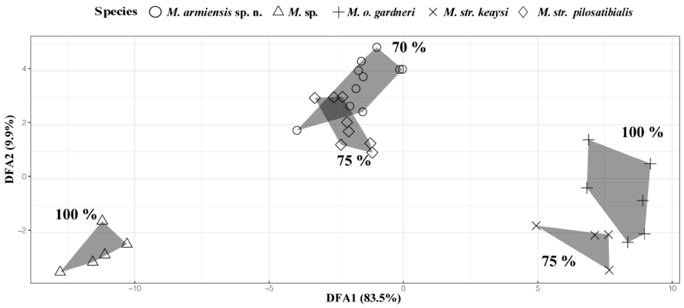

Figure 5. Vector correlation coefficients (loadings) between original variables and discriminant functions (DF1, DF2), with jackknifed percentage of correctly classified specimens for each group. Samples:*M. armiensis* sp. n (circles), *M.* sp (triangles), *M. oxyotus gardneri* (+ symbol), *M. keaysi str.* (x symbol), and *M. pilosatibialis str.*(diamonds).

Annual Temperature was the principal driver of PC3. One-way multivariate analysis of variance suggested there was a statistically significant difference on PC1, PC2, and PC3 as suggested by Pillai's Trace test, $F_{(6, 30)} = 2.283$, $P < 0.1$. Follow-up ANOVAs showed that this dissimilarity occurred at PC3 $F_{(2, 16)} = 4.32$, $P < 0.5$, but not for PC1 $F_{(2, 16)} = 1.50$ ns and PC2 $F_{(2, 16)} = 1.50$ ns. Post-hoc multiple comparison analyses did not reveal statistically significant differences in the climatic envelopes of all species, as indicated by extensive overlap (Figure 6; Table 4).

Discussion

In this report we were able to determine the phylogenetic placement of *M. pilosatibialis str.* based on specimens from Alta Verapaz, Guatemala (San Pedro Carcha, Finca Bethel, 15° 0.61′ N, -90° 0.27′ W), the collecting locality for specimens included in the subspecies description (La Val 1973). This locality is *ca.* 370 km from the type locality at Francisco Morazán, Honduras (14° 0.24 ′N, -85° 0.5′ W), therefore we recommend assigning the name *pilosatibialis* to this species complex, which has a disjunct distribution (primarily low and high elevation species) from southern México, southeastward through Central America into northwestern Panamá, and to the eastern cordillera of the Colombian and Cordillera Oriental (Ecuador). Elsewhere, this complex occurs from the island of Trinidad, to Venezuela and the Colombian Caribbean. This group is characterized by small to medium size, with short woolly hair, and the dorsal surface of tibia partially or entirely covered by fur, which might extend to the hindfoot and across the tibia and onto the plagiopatagium. A flattened occipital region and moderate to high sagittal crest characterize the skull. In agreement with Moratelli *et al.* (2016) and Moratelli *et al.* (2017), we included *pilosatibialis* as part of the *ruber* group based on shared morphological traits (woolly hair, moderate to high sagittal crest, and flat occipital crest) and close molecular evolutionary proximity. Likewise, we determined the phylogenetic placement of *M. keaysi str.*, from voucher specimens collected in Cochabamba, Bolivia (-17° 0.21′ S, -65° 0.6′ W), located ~ 600 km distant from the type locality of *M. keaysi* at Inca Mines, Cuzco, Perú (-13° 0.30 ′ S ,-70 ° 0.0 W). *Myotis keaysi* is another member of the *ruber* group, with larger external and cranial dimensions, and longer woolly fur, now suggested to be distributed in high elevation sites from the Andes of Colombia, southward to Bolivia and Argentina (Moratelli *et al.* 2013). According to Mantilla-Meluck and Muñoz-Garay (2014) both species are living in sympatry in the Colombian Caribbean and eastern cordillera of the Andes of Colombia.

Larsen *et al.*'s (2012 a, b) molecular study of Neotropical *Myotis* identified an unnamed clade formed by specimens misidentified as *M. nigricans* (TTU 39146 from Santa Clara, Chiriquí, Panamá) and *M. riparius* (TTU 85060 from Azuay, Tungurahua, Ecuador) collected by Robert J. Baker and collaborators in 1983 (Panamá) and 2001 (Sowell-Expedition, Ecuador). Chaverri *et al.* (2016) referred to this clade as *M. keaysi* based on cytochrome *c* oxidase subunit I sequences of unvouchered specimens from Valle del Silencio, Costa Rica and one specimen (ROM 104302), collected by the Royal Ontario Museum in Santa Clara, Ojo de Agua, 2 km N of Santa Clara, Panamá.

Prior to those studies, voucher specimen series of *Myotis* collected from the highlands of Chiriquí Province (USNM, TCWC) had been identified as *M. k. pilosatibialis*. Our bat surveys (in Ecuador in 2017 and Panamá in 2012) provided additional specimens for morphological and genetic studies. Herein, we have examined specimens assigned to the unnamed clade *sensu* Larsen *et al.* (2012 a, b), and found morphometric and genetic differences that support recognition of a new species. We propose that populations from Chiriquí Province (Panamá) and Cordillera Oriental (Ecuador) represent a new species, which is described as follows:

Myotis armiensis, species novum

Armien's Myotis, Myotis de Armién

Figure 7, 8, and 9; Tables 5 and 6

Myotis keaysi pilosatibialis, La Val, 1973, part

Myotis keaysi pilosatibialis, Hernandez-Meza *et al.* 2005, part.
Myotis keaysi pilosatibialis, Wilson, 2008, part.
Myotis nigricans, Larsen et *al*. 2012a, part.
Myotis riparius, Larsen et *al*. 2012b, part.
Myotis keaysi, Chaverri et *al*. 2016, part.
Myotis cf. *pilosatibialis*, Moratelli et *al*. 2016, part.
Myotis cf. *pilosatibialis*, Moratelli et *al*. 2017, part.

Holotype and type locality. Voucher MSB 262089; adult male; preserved as skin, skull and skeleton (Figures 8 and 9) at the Museum of Southwestern Biology (MSB), University of New Mexico collected on 20 March 2012 by Joseph A. Cook and collaborators (Tropical Biology Class 2012 and Instituto Conmemorativo Gorgas de Estudios de la Salud) at La Amistad International Park Ranger Station (8° 89′ N, -82° 61′ W, elevation 2, 214 m), Bugaba District, Chiriquí Province, Panamá. Tissues deposited at the same museum (NK 209314, LN2 preservation), with additional tissues at Instituto Gorgas, Panama City (-80°C preservation). The specimen is well preserved. The measurement for the forearm (44 mm) recorded on the specimen tag is incorrect and should be FA = 39 mm as now recorded in the Arctos Museum Database.

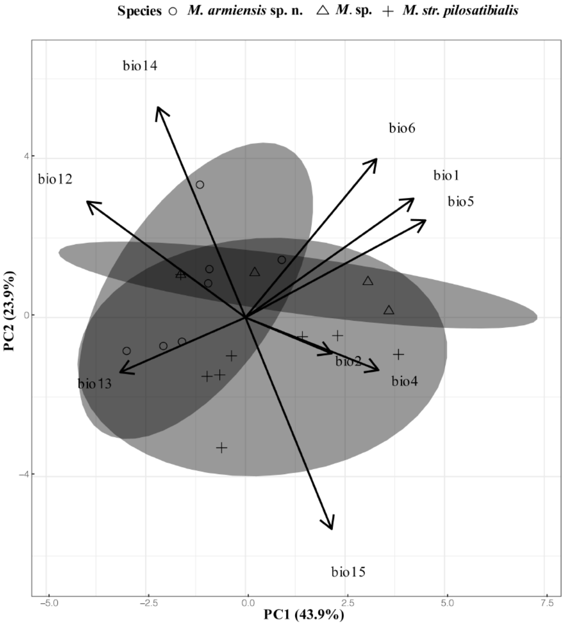

Figure 6. Principal component (PC´s) from a PCA based on 9 bioclimatic variables extracted from 19 distribution localities of *pilosatibialis* species complex, with confidence ellipses and corresponding vectors correlations of climatic variables with the first two eigenvectors. Samples:*M. armiensis* sp. n. (circles), *M.* sp. (triangles), and *M. pilosatibialis str.*(+ symbols).

Figure 7. Adult female of *Myotis armiensis* sp. n. (QCAZ 17245) captured at Cabañas del Aliso, Cosanga, Napo Province, Ecuador. Photographed by Carlos Carrión Bonilla.

Paratypes. Nineteen additional specimens were collected from Chiriquí Province, Panamá and Cordillera Oriental (Ecuador). Two specimens were designated as paratypes based on genetic identification, (partial cytochrome *b*), morphometrics and qualitative data: skin of one adult female (MSB 262085), collected by Joseph A. Cook and collaborators, 20 March 2012; skin and skull of one female, adult (TTU 85060) collected by Robert J. Baker and collaborators (Sowell Expedition-Ecuador, 2001), 24 July 2001.

Six paratypes identified solely by genetic identification (partial cytochrome *b*) were collected at Bugaba District, Chiriquí Province, Panamá [one adult male (MSB 262237) collected by Joseph A. Cook and collaborators, 20 March 2012)], Jurutungo, Río Sereno, Renacimiento District, Chiriquí Province, Panamá [sex unknown (MSB 262788), collected by Gorgas Institute field researchers, 6 May 2011], Santa Clara, Renacimiento District, Chiriquí Province, Panamá [one female, age unknown (TTU 39146), collected by Robert J. Baker, 19 January 1983], Cabañas del Aliso, Cosanga, Napo Province, Ecuador [one female, age adult, (QCAZ 17245) collected by Carlos A. Carrión Bonilla, 13 December 2017), Yantzaza, Campo Minero Fruta del Norte, Zamora Chinchipe, Ecuador [male, adult (QCAZ 12461), collected by Paula Iturralde, 3 March 2011]. Another specimen from Ojo de Agua, 2 km N of Santa Clara, Renacimiento District, Chiriquí Province, Panamá (ROM 104302), collected by Burton Lim and Eamon O'Toole, on 8 March 1995 was identified based on barcode cytochrome *c* oxidase subunit I.

Table 4. Factor loading after PCA and varimax rotation, with Kaiser Normalization for three principal components from a principal component analysis (PCA). The analysis is based on 9 bioclimatic variables, including 19 localities.

Climatic variable	PC I	PC II	PCIII
Annual Mean Temperature	.972	.209	.086
Mean Diurnal Range	-.013	.697	.027
Temperature Seasonality	.242	.633	.287
Max Temperature of the Warmest Month	.923	.337	.128
Min Temperature of the Coldest Month	.988	-.037	-.036
Annual Precipitation	-.157	-.820	-.480
Precipitation of the Wettest Month	-.241	-.883	.243
Precipitation of the Driest Month	-.048	-.086	-.965
Precipitation Seasonality	.047	.073	.973
eigenvalues	2.9	2.5	2.2
% of variance explained	32.4	27.8	25.3
cumulative %	32.4	60.2	85.6

Ten paratypes identified with morphometric analysis of craniometric measurement analysis and qualitative morphological of skins and skulls were collected from La Amistad International Park Ranger Station, Bugaba District, Chiriquí Province, Panamá [(two females, adults (MSB 262217-18, only skins were studied, no skulls available) collected by Joseph A. Cook and collaborators, 20 March 2012)]; Cerro Punta, Casa Tiley, Tierras Altas District, Chiriquí Province, Panamá [female, adult (USNM 323599, by Handley, C. and Greenwell, F.M., 6 March, 1962)]; El Volcán 2 min S. W, Tierras Altas District, Chiriquí Province, Panamá [two females, adults, (USNM 331942, USNM 331943, by Tyson E, collected 21 March 1962)]; Cuesta de Piedra, Tierras Altas District Chiriquí Province, Panamá [female, adult (USNM 331953, by Tyson E, 28 March 1962)]; 36 km, north of Concepción, Bugaba District, Chiriquí Province, Panamá [five females, adults (TCWC 12655-59, by Patten, D.R., 8 June 1964)]. We did not include any specimens from Costa Rica in the type series, because the Chaverri *et al.* (2016) study was unvouchered, and therefore morphological confirma-

Table 6. Selected measurements, cranial index, body mass (adults males and females[*N*]). Mean, (Minimum–Maxima) and sample size (*n*). See methods for variable abbreviations.

Characters	***M. armiensis sp. n.*** **Chiriquí (Panamá) and Cordillera Oriental (Ecuador)**	***M. keaysi str.*** **Perú**	***M. pilosatibialis str.*** **El Salvador Honduras México**	***M. sp.*** **Quintana Roo, Yucatán, México**	***M. oxyotus gardneri*** **Costa Rica and Panamá**
Body mass	5.0 (4.5–5.6) *n* = 10	6.0 *n* = 1	6.1 *n* = 1		8 *n* = 1
HB	86 (77–92) *n* = 12	94.0 *n* = 1			93.0 (87–98) *n* = 3
Tail	39 (32–48) *n* = 13	42.0 *n* = 1			40.3 (39–43) *n* = 3
Foot	8 (7–10) *n* = 13	8.0 *n* = 1			8.3 (8–9) *n* = 3
Ear	13 (11–14) *n* = 13	14.0 *n* = 1			15.7 (15–16) *n* = 3
LDF	6.2 (5.3–7.4) *n* = 10				7.7 (7.4–7.9) *n* = 3
LVF	6.3 (4.5–8.3) *n* = 10				6.6 (5.6–7.2) *n* = 3
FA	38.0 (36.3–39.4) *n* = 13	40.2 *n* = 1	35.9 (34.3–37.1) *n* = 5	32.6 (31.8–34.4) *n* = 4	40.4 (38.0–42.8) *n* = 6
3MC	34.3 (32.9–35.9) *n* = 13	36.8 *n* = 1	33.2 (32.1–34.4) *n* = 5	29.3 (27.7–30.4) *n* = 4	36.3 (34.5–38.6) *n* = 6
GLS	13.5 (13.0–14.0) *n* = 10	14.5 (14.1–15.0) *n* = 5	13.6 (13.5–13.9) *n* = 8	12.7 (12.6–13.0) *n* = 4	14.5 (14.1–15.0) *n* = 6
CCL	12.1 (11.7–12.5) *n* = 10	12.6 (12.0–13.0) *n*= 5	12.1 (11.8–12.3) *n* = 8	11.4 (11.2–11.7) *n* = 4	12.8 (12.3–13.3) *n* = 6
CBL	12.7 (12.3–13.0) *n* = 10	13.3 (12.6–13.8) *n* = 5	12.7 (12.4–12.9) *n* = 8	12.1 (11.7–12.4) *n* = 4	13.5 (13.1–14.1) *n* = 6
CIL	12.7 (11.9–13.2) *n* = 10	13.5 (12.9 –14.0) *n* = 5	12.9 (12.7–13.1) *n* = 8	12.1 (11.8–12.5) *n* = 4	13.7 (13.2–14.2) *n* = 6
BAL	11.7 (11.3–12.1) *n* = 10	12.1 (11.5–12.5) n = 5	11.6 (11.3–11.9) *n* = 8	11.0 (10.7–11.3) *n* = 4	12.4 (12.0–12.8) *n* = 6
ZB	8.5 (7.9–8.8) *n* = 8	8.6 (8.5–8.8) *n* = 4	8.2 (8.1–8.4) *n* = 6		8.9 *n* = 1
MAB	7.0 (6.6–7.4) *n* = 10	7.0 (6.9–7.2) *n* = 5	7.0 (6.9–7.2) *n* =8	6.7 (6.6–6.7) *n* = 4	7.3 (7.1–7.4) *n* = 6
BCB	6.8 (6.2–7.3) *n* = 10	6.5 (6.4 –6.5) *n* = 5	6.3 (6.1–6.5) *n* =8	5.9 (5.8–6.0) *n* = 4	6.8 (6.6–7.0) *n* = 6
IOB	4.5 (4.2–4.8) *n* = 10	4.7 (4.5–4.9) *n* =5	4.3 (4.2–4.5) *n* = 8	4.0 (3.9–4.1) *n* = 4	4.7 (4.5–4.9) *n* = 6
POB	3.6 (3.2–4.2) *n* = 10	3.6 (3.4–3.8) *n* = 4	3.4 (3.3–3.5) *n* = 8	3.1(3.1–3.2) *n* = 4	3.9 (3.8–4-0) *n* = 6
BAC	3.6 (3.4–4.0) *n* = 10	3.6 (3.5–3.7) *n* = 5	3.6 (3.5–3.8) *n* = 8	3.3 (3.2–3.4) *n* = 4	3.6 (3.4–3.8) *n* = 6
BAM	5.5 (5.3–6.0) *n* = 10	5.6 (5.4–5.8) *n* = 5	5.3 (5.2–5.5) *n* = 8	4.9 (4.7–5.0) *n* = 4	5.7 (5.5–5.8) *n* = 6
MTL	5.2(5.1–5.4) *n* = 10	5.5 (5.2–5.6) *n* = 5	5.1(5.0–5.2) *n* = 8	4.8(4.6–4.9) *n* = 4	5.5 (5.4–5.6) *n* = 6
M1–3	2.9 (2.5–3.0) *n* = 10	3.1 (3.0–3.3) *n* =5	2.9 (2.8–3.0) *n* = 8	2.6 (2.5–2.6) *n* = 4	3.1 (3.1–3.2) *n* = 6
MAL	9.6 (8.9–10.3) *n* = 10	10.2 (9.9–10.5) *n* =5	9.6 (9.5–9.7) *n* = 8	9.1 (8.8–9.3) *n* = 4	10.4 (10.0–10.9) *n* = 6
MAN	5.5 (5.3–5.7) *n* = 10	5.8 (5.6–5.9) *n* = 5	5.5 (5.4–5.7) *n* =8	5.1 (4.9–5.2) *n* = 4	5.7 (5.7–5.9) *n* = 6
CRI	50.6 (47.0–53.7) *n* = 10	51.5 (49.7–53.9) *n* = 5	47.3 (45.8–49.1) *n* = 8	42.1 (41.1–43.3) *n* = 4	53.8 (50.7–56.0) *n* = 6
MAX	18.1 (17.2–19.6) *n* = 10	18.8 (17.6–19.9) *n* = 5	17.3 (16.7–17.9) *n* = 8	15.0 (14.0–15.5) *n* = 4	19.2 (18.4–19.8) *n* = 6

tion is not possible.

Distribution. *Myotis armiensis* sp. n. is known from the premontane and montane forest of Chiriquí Province, Panamá, extending its distribution into La Amistad International Park in Panamá (Las Nubes Rangers Station) and Costa Rica (Valle del Silencio). Elevation in Panamá and Costa Rica varies from 975 m to 2,500 m: Concepción (≈ 8°.51′ N, -82°.62′ W, 2,011m), Cerro Punta (8°.88′ N, -82°.73′ W, 1,280 m), Cuesta de la Piedra (8°.88′ N, -82°.73′ W, 975 m), El Volcán (8°.88′ N, -82°.73′W, 1,280 m), Parque Internacional la Amistad Ranger Station: (8°.89′ N, -82°.61 W, 2, 214 m), Jurutungo, Río Sereno (8°.9′ N, -82°.73 W, 2,219 m),

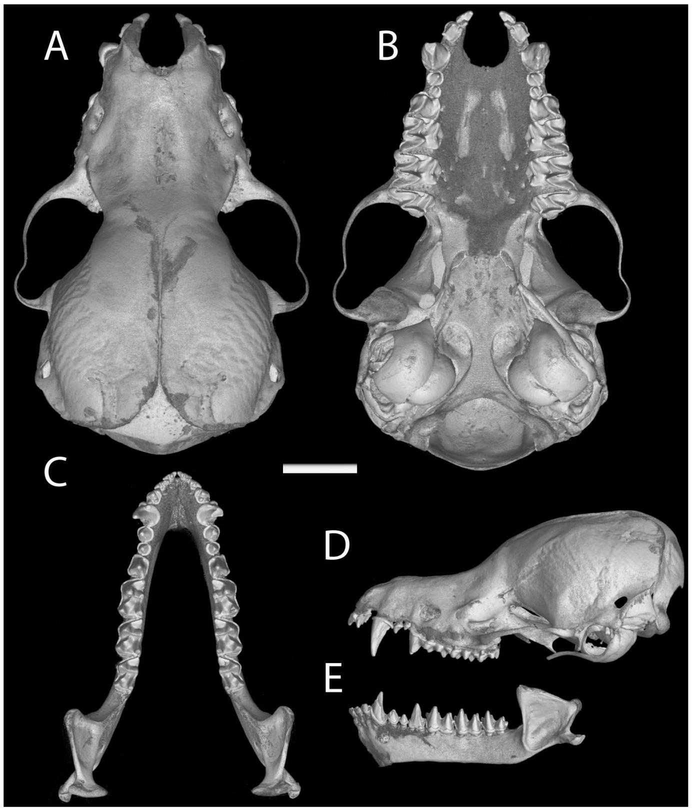

Figure 8. Dorsal (A) and ventral view (B) of the cranium, dorsal view of the mandible (C), and lateral view of the cranium (D) and mandible of the holotype of *M. armiensis* sp. n. (MSB 262089). Scale bar = 5 mm. Photograph taken by John Korbin (Sandia National Laboratory-New Mexico, USA).

Table 5. Selected measurements (mm) and body weight (g) of the holotype (MSB 262089) and paratype material of *Myotis armiensis*. See methods for variable abbreviations.

Characters	MSB 262089 ♂	Paratypes
Body mass	5	5 (4.5–5.6) *n* = 9
HB	90	85 (77–92) *n* = 11
Tail	38	39 (32–48) *n* = 12
Foot	8	8 (7–10) *n* = 12
Ear	13	14 (11–14) *n* = 12
LDF	6.4	6.1 (5.3–7.4) *n* = 9
LVF	7.2	6.2 (4.5–7.4) *n* = 9
FA	37.1	38.1 (36.3–39.4) *n* = 12
3MC	34	34.3 (32.9–35.9) *n* = 12
GLS	13.3	13.5 (13.0–14.0) *n* = 9
CCL	12.2	12.1 (11.7–12.5) *n* = 9
CBL	12.3	12.8 (12.5–13.0) *n* = 9
CIL	11.9	12.8 (12.2–13.2) *n* = 9
BAL	12.1	11.6 (11.3–11.9) *n* = 9
ZB	7.9	8.6 (8.0–8.8) *n* = 7
MAB	6.6	7.1 (6.6–7.4) *n* = 9
BCB	7.3	6.8 (6.2–7.2) *n* = 9
IOB	4.4	4.6 (4.2–4.8) *n* = 9
POB	4.2	3.5 (3.2–3.7) *n* = 9
BAC	3.6	3.7 (3.4–4.0) *n* = 9
BAM	5.4	5.6 (5.3–6.0) *n* = 9
MTL	5.2	5.2 (5.0–5.4) *n* = 9
M1–3	2.7	2.9 (2.5–3.0) *n* = 9
MAL	9.5	9.6 (8.9–10.3) *n* = 9
MAN	5.7	5.5 (5.3–5.7) *n* = 9

Santa Clara (≈ 8°.83′ N, -82°.75′ W, ≈ 1,178 m), Ojo de Agua, Santa Clara (8° 42′ N, -82°.45 W, 1,500 m), Valle del Silencio, Costa Rica (9° 11′ N, -82°.96 W, 2,500 m). In Ecuador, *M. armiensis* sp. n. is known from Cordillera Oriental. Elevation in Ecuador varies from 1,200 m to 2,249 m: Yantzaza, Campo Minero Fruta del Norte, Zamora Chinchipe (-3°.75′ S, -78°.53′ W, 1, 200 m), Colonia Azuay, Tungurahua Province, Ecuador (-1°.34′ S, -78.20°, 1,660 m), Cabañas el Aliso, Sector Las Caucheras, Quijos, Napo Province (-3°.75′ S, -78°.53′ W, 2,249 m). See Figure 10 for species distribution in Costa Rica, Panamá and Ecuador.

Etimology. *Myotis armiensis* honors Dr. Blas Armién in recognition of his outstanding contributions to research in zoonotic emergent diseases, public health, and mammalogy in Panamá. Over two decades, he has supported the systematic development of holistic museum collections, including associated cryogenic biorepositories and parasites. This infrastructure (>11,000 specimens) is now the basis for new insights into temporal and spatial aspects of the biology of Panama's mammals and associated parasites and pathogens.

Diagnosis. Due to the dearth of availability of substantial specimen material and despite the lack of a single morphological character that consistently distinguishes *M. armiensis* from the rest of Neotropical congeners, *Myotis armiensis* can be distinguished by a combination of the following morphological traits: pelage is short and woolly, dorsal and ventral fur bicolored; insertion of the plagiopatagium occurs on the foot at the level of the base of toes by a wide membrane; lack or relatively low presence of fur on dorsal surface of tibia, foot and plagiopatagium, and border of the uropatagium without a fringe; skull is moderately large; forehead is steeply sloping; rostrum is long; lambdoidal crest is present and high; sagittal crest present, with height from low to medium; occipital crest is absent; occipital region flattened and the shape of the braincase is globular.

Myotis armiensis can be readily distinguished from *Myotis* congeners from Central and South America based on gene trees [partial sequence of cytochrome-*b* (~710 pb) and partial cytochrome *c* oxidase subunit I (~ 657 pb)] and species tree phylogenetic analysis of one exon: recombination activating gene II (RAG2), and 3 intron regions: protein kinase C, iota (PRKCI), signal transducer and activator of transcription 5A (STAT5A), and thyrotropin (THY). Finally, molecular synapomorphies in mitochondrial and intron genes regions sequences support the species level recognition of *M. armiensis* sp. n. compared to other species in the New World *Myotis* radiation (Appendix VI– X). These served as diagnostic characters for the species.

Description. A medium to large species of *Myotis* (FA 36.3–39.4 mm, *n* = 13 and weight 4.5-5.6 gr, *n* = 10); other

Figure 9. Dorsal and ventral views of the skins of the holotype of *M. armiensis* sp. n. (MSB 262089), *M. pilosatibialis str.*(TCWC 24101, paratype), and *M. keaysi str.* (MSB 70381). Scale bar = 10 mm.

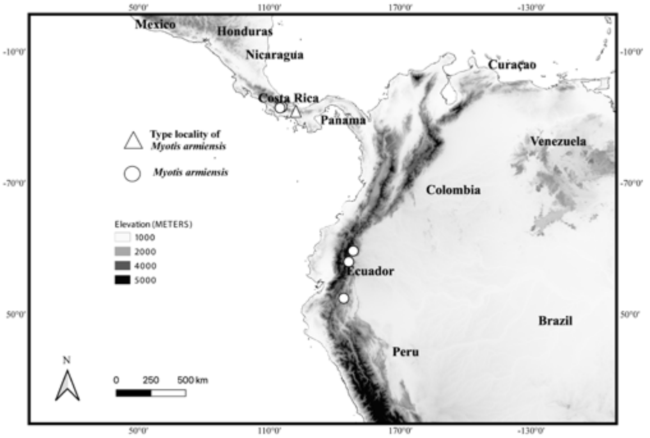

Figure 10. Map of part of Central and South America showing localities examined for *M. armiensis*, with triangle (type locality) and distribution in Costa Rica, Panamá, and Ecuador with circles. See Appendix I for localities of examined in Panamá and Ecuador.

measurements (Tables 5 and 6), with external size larger than *M. pilosatibialis str.*, *M.* sp. (Quintana Roo, México) and smaller than *M. oxyotus gardneri*, and *M. keaysi str*. Ears are brown in color, comparatively small to medium-sized (EL 11–14 mm). Dorsal and ventral fur is woolly and short (LDF 5.3 -7.4 mm, LVH 4.5-8.3 mm). Dorsal pelage is bicolor, with brown to dark brown at the base and from brown to Mummy Brown at the tips. Ventral pelage is bicolor, with Buckthorn Brown to buff at the tips and dark brown to black at the base. Abdomen is bicolor, from Buckthorn Brown to black with buff tips. Sides and wing color are dark brown or Cinnamon Brown to Mummy Brown. Uropatagium and plagiopatagium are Mummy Brown or Cinnamon Brown. Insertion of the plagiopatagium occurs at the foot at the level of the base of toes by a wide membrane. The uropatagium lacks fringing hairs along the trailing edge. Fur presence on tibia, foot and plagiopatagium, with fur extending across a quarter or less than this at the base of the dorsal and ventral side of uropatagium. Skull and mandible are medium-size (GLS 13.0 –14.0 mm, MAL 8.3–10.3). The dental formula is: 2/3, 1/1, 3/3, 3/3 = 38. In the holotype, the second upper premolar (p3) is aligned and visible in lateral view. Rostrum is long and frontals are steeply sloping; lambdoidal crest is well developed and occipital region is flattened.

Comparisons. In comparison with species in the *ruber* group, *M. armiensis* sp. n. differs from *simus* and *riparius* by having a less contrasting dorsal and ventral coloration (dorsal fur with dark brown to Mummy Brown and ventral fur with Buckthorn Brown to dark brown), with more contrasting (Orange-Brown or Chocolate) in *simus*, (golden -yellow) in *midastactus*, (ventral hairs with dark brown based and yellowish tips/reddish-brown or cinnamon brown dorsal color) in *riparius*, (Bister Brown color of dorsal hairs at tips and buff to orange of ventral color at tips) in *pilosatibialis* [type material]. *M. armiensis* sp. n. can be distinguished from *keaysi* by having shorter woolly hair on dorsal and ventral side, with longer woolly hair, larger proportion of fur on dorsal and ventral side of the uropatagium, and furrier tibia in *keaysi*. It differs from *simus* by having the plagiopatagium attached broadly to the side of the foot at the level of the toes; with a narrow band of membrane (< 1.5 mm) attached to foot or ankles and with extremely short and woolly fur in *simus*. *M. armiensis* sp. n. shares the flattened occipital region and a moderate to high sagittal crest with members of the *ruber* group. It can be distinguished from *M. ruber* by presence of woolly hair, with silky pelage in *ruber*. Cranial index of *M. armiensis* sp. n. is only larger that *M. pilosatibialis str.* but smaller than other congeners in the *ruber group* (CRI: *armiensis* = 47.0–53.7 , *pilosatibialis* = 45.8–49.1, *keaysi* = 49.7–53.9; *simus* = 73.0–88.1; *ruber* = 78.4–85.0; *riparius* = 64.6–76.1), reflecting a narrower skull configuration.

Myotis armiensis sp. n. differs from the *albescens* group (*albescens*, *handleyi*, *nesopolus*, *nigricans*, *oxyotus oxyotus*, *oxyotus gardneri*, *izecksohni*, *lavali* and *levis*) by having short woolly hair. It only shares the woolly hair trait with *chiloensis*. In addition, it can be distinguished from *albescens* group by the presence of a moderate sagittal crest [absent in *albescens*, very low or absent in *oxyotus*, absent in *nigricans* or very low, absent in *lavali*, very low in *chiloensis*]. *Myotis armiensis* sp. n. differs from *levis* and *albescens* by the absence of fringe of hairs along the edge of the uropatagium. Occipital region is flattened in *M. armiensis* sp. n. [rounded in *albescens*, *oxyotus*, *lavali*, *nigricans*]. The cranial index for *albescens* group is larger than *M. armiensis* sp. n, having the narrowest skull configuration in comparison with this species group.

Reproductive data. One pregnant female with one embryo (MSB 262085) collected by Joseph A. Cook and collaborators at Las Nubes Ranger Station, La Amistad International Park, 20 March 2012. Another female (USNM 323599) with embryo (crown-rump = 3 mm) collected at Cerro

Punta, Casa Tiley, Chiriquí Province, collected by Greenwell, F. M, 6 March 1962. In Ecuador, one pregnant female (TTU 85060) with embryo (crown-rump = 3 mm) collected by Robert J. Baker and collaborators (Sowell-Expedition, 2001) at Colonia Azuay, Tungurahua Province, 24 July, 2001.

Habitat and ecological notes. Las Nubes Ranger Station, the type locality for this new species, is part of a natural corridor (401, 000 ha) of relatively undisturbed montane habitats of the eastern Talamanca Mountains that rise between the Pacific and Caribbean coastlines of Panamá and Costa Rica (Morrone 2017). At La Amistad International Park, Las Nubes Ranger Station, *M. armiensis* sp. n. was found to occur sympatrically with *Desmodus rotundus*, *Anoura geoffroyi*, *Sturnira* cf. *burtonlimi*, *Sturnira mordax*, *Enchistenes hartii* (Phyllostomidae), and *Tadarida brasiliensis* (Molossidae). All captures in 2011, 2012 were with ground mist nets located on the edge of secondary growth forest near Las Nubes Rangers Station. Specimens were collected at a clearing on the edge of the forest (Cerro Punta, Casa Tiley) and in montane forest near a lake shore and moist montane secondary growth forest (2 miles S. W of El Volcán). We did not record any other species of *Myotis* living in sympatry at La Amistad International Park, but based on historic samples, the nominal subspecies *M. oxyotus gardneri* was found in sympatry with the new species at Cerro Punta and El Volcán.

At Valle del Silencio Costa Rica, *M. armiensis* sp. n. was found with *Sturnira burtonlimi*, *Dermanura tolteca*, *Hylonycteris underwoodi*, *Anoura cultrata* (Phyllostomidae), and *Lasiurus blossevillii, Myotis* cf. *nigricans*, and *M. oxyotus gardneri* (Vespertilionidae). The vegetation there was characterized by the presence of oak trees (*Quercus* spp) and bamboo (*Chusquea spp*.), although some sites at Valle del Silencio were dominated by swampy bogs (Chaverri *et al.* 2016).

In Ecuador, *M. armiensis* sp. n. is known from premontane and montane cloud forest of Cordillera Oriental. These forests correspond to Evergreen Lower Montane Forest and Cloud Montane Forest (Bosque Siempreverde Montano Bajo and Bosque de Neblina Montano; Valencia *et al.* 1999). One specimen of *M. armiensis* sp. n. was netted across a trail leading to secondary growth forest in Cabañas del Aliso, Cosanga, Quijos Valle, Napo Province in December, 2017. Other species captured in sympatry at that location were: *Sturnira bogotensis*, *Carollia brevicauda* (Phyllostomidae), *Tadarida brasiliensis* (Molossidae), and *M. oxyotus oxyotus* and *Histiotus montanus* (Vespertilionidae). The vegetation there was characterized by the presence of epiphytes (moss, ferns, orchids, bromeliads) , bamboo (*Chusquea spp*.), and pepper plants (*Piper spp*. and *Peperomia spp*.). Another specimen of *M. armiensis* sp. n. was captured in Colonia Azuay, Tungurahua Province at the north side of the Río Pastaza. This locality is bisected by the Río Topo, a tributary of the Pastaza river and comprises secondary forest and fruit orchards (Haynie *et al.* 2006). Other bat species captured in sympatry at that location were: *Anoura caudifer*, *Artibeus lituratus*, *Carollia perspicillata*, and *Sturnira erythromus*. (Phyllostomidae).

Remarks. It was not possible to examine a set of fluid preserved specimens (*n* = 43) collected at La Amistad International Park Ranger Station, Bugaba District, Chiriquí Province, collected in 2018 by Joseph A. Cook and collaborators (Tropical Biology Class 2018 and Gorgas Institute field workers). Those specimens, until recently housed at the Gorgas Institute in Panama, may represent *M. armiensis* sp. n., but confirmation will require further molecular and morphological analysis (MSB 262086 –88, MSB 262219–262224, 268090–93, MSB 327505–327516, MSB 327520, MSB 327522 –327527, MSB 327575–578, MSB 327601–602, MSB 327649–50, MSB 327700, MSB 327703, MSB 327705, MSB 327709, MSB 327712, MSB 327956).

Based on this report and other museum collections records, the diversity of *Myotis* comprises at least six species in Panamá: *M. albescens*, *M. oxyotus gardneri*, *M. riparius*, *M. pilosatibialis*, *M. nigricans s.l.*, and *M. armiensis* sp. n. In Ecuador, the recognition of this newly identified lineage, increases the diversity to eight species of *Myotis*: *M. albescens*, *M. riparius*, *M. simus*, *M. oxyotus oxyotus*, *M. diminutus*, *M. keaysi*, *M. nigricans s.l.*, and *M. armiensis* sp. n. In Costa Rica*, Myotis* diversity increases to seven species: *M. elegans*, *M. riparius*, *M. albescens*, *M. pilosatibialis*, *M. nigricans s.l.*, *M. oxyotus. gardneri* and now *M. armiensis* sp. n.

Nomenclatural statement.— A life science identifier (LSID) number was obtained for new species described herein: urn:lsid:zoobank.org:pub:9EB39E62-C9AC-41C0-AE76-9C5325608BEE.

Conservation. Myotis armiensis sp. n. is restricted to higher and cooler mountain forest of Panamá, Costa Rica and Cordillera Oriental (Ecuador). These habitats are susceptible to the effects of climate change, in addition to ongoing habitat destruction. This report aims to contribute to efforts to study these environments and more narrowly add to our understanding of species limits of this elusive group of bats.

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We would like to honor S. Anderson for demonstrating throughout his life of fieldwork in mammalogy (extending from Janos, Chihuahua to Tarija, Bolivia) the immense, multifaceted, and lasting value of each voucher specimen to science and society. Likewise, we especially like to thank R. Moratelli for providing access to morphological and morphometric data from Central America and South American *Myotis*. The completion of this research would have not been possible without his generous offer of this information. We would like to thank also P. A Menendez (McGill University, Canada) for his help with statistical analyses. The following curators and collection managers provided access to specimens under their care: S. Burneo, A. Camacho (Museo de Zoología QCAZ-Pontificia Universidad Católica del Ecuador, Quito-Ecuador); B. Patterson (Field Museum of Natural History, Chicago); E. Lacey, J. Patton, C. Conroy (Museum of Vertebrate Zoology, Berkeley); J. Dunnum and M. Campbell (Museum of Southwestern

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Appendix 1. Specimens examined in morphological and morphometric analysis. Specimens are organized according to taxa herein recognized. These vouchers consist of fluid preserved specimens, stuffed skins, and skulls deposited in the following institutions: American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Natural History Museum, University of Kansas (KU); Natural History Museum of Los Angeles County, Los Angeles, (LACM); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museum of Southwestern Biology, University of New Mexico (MSB); National Museum of Natural History, Smithsonian Institution (USNM); Museo de Zoología, División de Mastozoología, Pontificia Universidad Católica del Ecuador (QCAZ), Royal Ontario Museum (ROM); Sam Noble Oklahoma Museum of Natural History, University of Oklahoma (SNOMNH); Texas A&M Biodiversity Research and Teaching Collection, College Station (TCWC); Museum of Texas Tech University (TTU). Localities are arranged alphabetically by species and major political units. Specimens marked with asterisks were included in the principal component and discriminant analyses.

Myotis albescens. ARGENTINA (*n* = 1): Tucumán, Trancas, km 42 on Hwy 364, S San Pedro de Colalao (SNOMNH 23790). PERU (*n* = 7): Uyacali, Balta, Río Curanja (MSB 28518-24).

Myotis armiensis sp. n. PANAMA (*n* = 16): Chiriquí, Bugaba, La Amistad International Park, Rangers Station (MSB 262089* [holotype], MSB 262085, MSB 262237 [paratypes]); Chiriquí, Bugaba, Renacimiento, Jurutungo, Río Sereno, La Amistad International Park (MSB 262788 [paratype]), Chiriquí, Renacimiento, Santa Clara (TTU 39146 [paratype]), Chiriquí, Renacimiento, Santa Clara, Ojo de Agua, 2 km N of Santa Clara (ROM 104302 [paratype]), Chiriquí, Tierras Altas, Cerro Punta, Casa Tiley (USNM 323599* [paratype]), Chiriquí, Tierras Altas, El Volcán 2 min SW (USNM 331942*, USNM 331943* [paratypes]), Chiriquí, Bugaba, 36 Km, North of Concepción (TCWC 12655-59* [paratypes]); ECUADOR (*n* = 3): Tungurahua Province, Azuay (TTU 85060 [paratype]), Napo Province, Cosanga, Cabañas del Aliso (QCAZ 17245 [paratype]), Zamora Chinchipe, Yantzaza, Campo Minero Fruta del Norte (QCAZ 12461[paratype]).

Myotis chiloensis. ARGENTINA (*n* = 1): 19 km N Villa La Angostura along Hwy 234 (SNOMNH 23496).

Myotis diminutus. ECUADOR (*n* = 1): Los Ríos, Rio Palenque Science Center. 47 km S (by road) of Santo Domingo de los Colorados (USNM 528569 [holotype]).

Myotis dinellii. ARGENTINA (*n* = 2): Salta, Guachipas, 7.8 km NNE Pampa Grande along Ruta Provincial 6 along Rio Cachi (SNOMNH 27933), Chubut, 3 km N Tecka along Hwy 40 (SNOMNH 23497).

Myotis keaysi. BOLIVIA (*n* = 1): Cochabamba Jachá Suyu (MSB 70381); PERU (*n* = 5): Puno Ocaneque, 10 mi N Limbani (MVZ 116050*); Cuzco, Cordillera Vilcabamba (AMNH 236134*, 233857*, 233854*, 214371*).

Myotis levis. BRASIL (*n* = 1): Sao Paulo, Estación Biológica Boraceia (FMNH 145327).

Myotis nigricans. BRASIL (*n* = 3) km 42 Antigua Rodavia Río-Sao Paulo. Iguatari Municipality, Rio de Janeiro (TCWC 22811-13 [neotypes]).

Myotis oxyotus oxyotus. ECUADOR (*n* = 3): Carchi, Gruta Rumichaca, 2 mi E La Paz (TCWC 12703-04, TCWC 12706 [neotypes]). PERU (*n* = 4) Huánuco, 10 Km N. Acomayo Bosque Unchog (MSB 49971-72); Huánuco 9 min S Huánuco (TCWC 12710-11).

Myotis oxyotus gardneri. COSTA RICA (*n* = 3) San José, Fila la Máquina (LSUMZ 12924* [holotype], 12917*,12929*). PANAMA (*n* = 3) Cerro Punta (USNM 318386*), Finca Lara (USNM 318869*, 318870*).

Myotis pilosatibialis. EL SALVADOR (*n* = 6) Ahuachapán, El Imposible, San Francisco Méndez (ROM 101273*), Santa Ana, Parque Nacional Montecristo, Bosque Nebuloso (ROM 101352*, 101357*, 101430*), Santa Ana, Parque Nacional Montecristo, Los Planes (ROM 101467*), Santa Ana, Hacienda Escuintla (TTU 60981*). HONDURAS (*n* = 7): Francisco Morazán, 1 km W of Talanga (LACM 36879* [holotype], TCWC 24101-24105 [paratypes]); Cortés, Omoa, 5.5 km southeast of Cuyamel, Santo Domingo (AMNH 265126). GUATEMALA (3): Petén Department, 12 km of Chinaja (KU 82105, 82108, 82109). MEXICO (*n* = 1): San Luis Potosí (TTU 35360*).

Myotis riparius. BOLIVIA (*n* = 1): Cochabamba, Sajta (MSB 70383); ARGENTINA (*n* = 1): Tucumán, Tafí Viejo. 5 km S.W. Siambon (SNOMNH 36220). ECUADOR (*n* = 1): Esmeraldas, Comuna San Francisco de Bogotá (TTU 102833). PARAGUAY (*n* = 1): Department of Canindeyu, Reserva Natural Privada Itabo (TTU 99378).

Myotis sp. MEXICO (*n* = 4) Yucatán Peninsula, Quintana Roo, Pueblo Nuevo (KU 91911*, KU 91912*, KU 91915*, KU 91916*).

Appendix 2. List of specimens used in cytochrome-*b* analyses of Neotropical *Myotis*. Specimens details, localities, and Genbank accession numbers of sampled individuals of Neotropical *Myotis*. Carnegie Museum of Natural History (CM); France (Catzeflis-Montpellier-V-); Field Museum of Natural History (FMNH); Jean-François Maillard (JFM DIREN); Kunico Kawai (KK); Museum National Histoire Naturelle (MNHN); The Angeles County Museum of Natural History (LACM); Museum of Vertebrate, Zoology, University of California Berkeley (MVZ); Museum of Southwestern Biology, The University of New Mexico (MSB); National Museum Prague (NMP); Osaka City University Graduate School of Medicine (OCUMS); Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ); T.H. Kunz (THK); Museum of Texas Tech University (TTU and TK); Universidad Autónoma Metropolitana-Iztapalapa (UAMI); University of Nebraska State Museum (UNSM).

Institution	Cat. No.	Species	GenBank	Country	Locality	Latitude	Longitude	Source
CM	63920	*Myotis albescens*	JX130444	Suriname	Nickerie	5.63	-56.79	Larsen *et al.* (2012a)
TTU	85088	*Myotis albescens*	JX130463	Ecuador	Pastaza	-1.44	-77.99	Larsen *et al.* (2012a)
TTU	85089	*Myotis albescens*	JX130464	Ecuador	Pastaza	-1.44	-77.99	Larsen *et al.* (2012a)
TTU	102363	*Myotis albescens*	JX130472	Ecuador	El Oro	-3.51	-80.13	Larsen *et al.* (2012a)
TTU	102348	*Myotis albescens*	JX130500	Ecuador	El Oro	-3.51	-80.13	Larsen *et al.* (2012a)
TTU	103744	*Myotis albescens*	JX130501	Ecuador	Guayas	-2.45	-79.62	Larsen *et al.* (2012a)
TK	151814	*Myotis albescens*	JK130586	Ecuador	Zamora-Chinchipe	----	----	Larsen *et al.* (2012a)
FMNH	162543	*Myotis albescens*	AF376839	Bolivia	Tarija	-21.78	-64.09	Ruedi and Mayer (2001)
FMNH	174926	*Myotis albescens*	MK799657	Perú	Maskoitania	-12.77	-71.38	Patterson *et al.* (2019)
TTU	46343	*Myotis albescens*	JX130445	Perú	Huánuco	-09.18	-75.59	Larsen *et al.* (2012a)
TTU	99124	*Myotis albescens*	JX130503	Paraguay	Boquerón	-21.73	-60.95	Larsen *et al.* (2012a)
TTU	99801	*Myotis albescens*	JX130502	Paraguay	Ñeembucú	-27.04	-57.86	Larsen *et al.* (2012a)
TTU	99818	*Myotis albescens*	JX130504	Paraguay	Ñeembucú	-27.04	-57.86	Larsen *et al.* (2012a)
MSB	262089	*Myotis armiensis* sp. n.	MW025265	Panamá	Chiriquí	8.89	-82.61	This study
MSB	262237	*Myotis armiensis* sp. n.	MW025266	Panamá	Chiriquí	8.89	-82.61	This study
MSB	262085	*Myotis armiensis* sp. n.	MW025268	Panamá	Chiriquí	8.89	-82.61	This study
MSB	262788	*Myotis armiensis* sp. n.	MW025267	Panamá	Chiriquí	8.89	-82.61	This study
TTU	39146	*Myotis armiensis* sp. n.	JX130435	Panamá	Chiriquí	----	----	Larsen *et al.* (2012a)
QCAZ	12461	*Myotis armiensis* sp. n.	MW025274	Ecuador	Zamora Chinchipe	-3.75	-78.53	This study
QCAZ	17245	*Myotis armiensis* sp. n.	MW025269	Ecuador	Napo	-0.62	-77.90	This study
TTU	85060	*Myotis armiensis* sp. n.	JX130514	Ecuador	Tungurahua	-1.34	-78.20	Larsen *et al.* (2012a)
MVZ	168933	*Myotis atacamensis*	AM261882	Perú	Olmos	-5.84	-79.82	Ruedi and Mayer (2001)
USNM ZM	29470	*Myotis attenboroughi*	JN020573	Tobago	St. George Parish	11.32	-60.55	Larsen *et al.* (2012b)
THK	002	*Myotis austroriparius*	AM261885	United States	Tennessee	35.51	-86.58	Stadelmann *et al.* (2007)
THK	I	*Myotis chiloensis*	AM261888	Chile	Santiago de Chile	-33.44	-70.66	Stadelmann *et al.* (2007)
TTU	109227	*Myotis clydejonesi*	JX130520	Suriname	Sipaliwini	4.43	56.12	Larsen *et al.* (2012a)
UAMI -TK (R. Lopez-Wilchis)	45364	*Myotis fortidens*	JX130439	México	Michoacán	----	----	Larsen *et al.* (2012a)
UAMI -TK (R. Lopez-Wilchis)	43134	*Myotis fortidens*	JX130437	México	Michoacán	----	----	Larsen *et al.* (2012a)
LACM	3713/LAF0030	*Myotis fortidens*	KC747690	México	Guerrero	----	----	Patrick & Stevens (2014)
THK	11500	*Myotis grisescens*	AM261892	USA	Tennessee	35.51	-86.58	Stadelmann *et al.* (2007)
TTU	48161	*Myotis* cf. *handleyi*	JN020569	Venezuela	Guárico	8.56	-67.57	Larsen *et al.* (2012b)
TTU	48170	*Myotis* cf. *handleyi*	JX130544	Venezuela	Guárico	8.56	-67.57	Larsen *et al.* (2012a)
TTU	48163	*Myotis* cf. *handleyi*	JX130531	Venezuela	Guárico	8.56	-67.57	Larsen *et al.* (2012a)
TTU	48164	*Myotis* cf. *handleyi*	JX130532	Venezuela	Guárico	8.56	-67.57	Larsen *et al.* (2012a)
TTU	48168	*Myotis* cf. *handleyi*	JX130533	Venezuela	Guárico	8.56	-67.57	Larsen *et al.* (2012a)
CM	78645	*Myotis* cf. *handleyi*	JX130535	Venezuela	Guárico	----	----	Larsen *et al.* (2012a)
TTU	48169	*Myotis* cf. *handleyi*	JX130543	Venezuela	Guárico	8.56	-67.57	Larsen *et al.* (2012a)
TTU	48166	*Myotis* cf. *handleyi*	JX130494	Venezuela	Guárico	8.56	-67.57	Larsen *et al.* (2012a)
QCAZ	11383	*Myotis keaysi*	JX130517	Ecuador	Chimborazo	----	----	Larsen *et al.* (2012a)
QCAZ	11380	*Myotis keaysi*	JX130516	Ecuador	Chimborazo	----	----	Larsen *et al.* (2012a)
MSB	70381	*Myotis keaysi*	MW025273	Bolivia	Cochabamba	-17.21	-65.86	This study
MVZ	185681	*Myotis lavali*	AF376864	Brazil	Paraiba	-7.11	-34.86	Ruedi and Mayer (2001)

FMNH	141600	*Myotis levis*	AF376853	Brazil	São Paulo	-23.53	-45.84	Ruedi and Mayer (2001)
MNHN	2005-895	*Myotis martiniquensis*	JN020557	Martinique, France	Grand'Rivière, Martinique	-14.87	-61.17	Larsen *et al.* (2012b)
V	2352	*Myotis martiniquensis*	JN020559	Martinique, France	Grand' Rivière, Martinique	-14.87	-61.17	Larsen *et al.* (2012b)
MNHN	2008-974	*Myotis martiniquensis*	JN020560	Martinique, France	Grand' Rivière, Martinique	-14.87	-61.17	Larsen *et al.* (2012b)
V	2354	*Myotis martiniquensis*	JN020561	Martinique, France	Grand' Rivière, Martinique	-14.872	-61.17	Larsen *et al.* (2012b)
JFM	DIREN 2	*Myotis martiniquensis*	AM262332	Martinique France	----	----	----	Stadelmann *et al.* (2007)
CM	98859	*Myotis* cf. *nigricans*	JX130453	Perú	Huánuco	-----	----	Larsen *et al.* (2012a)
CM	77691	*Myotis* cf. *nigricans*	JX130497	Suriname	Marowijne	----	----	Larsen *et al.* (2012a)
No voucher	-----	*Myotis nesopolus*	JN20575	Netherlands, Antilles	Bonaire	12.201	-68.26	Larsen *et al.* (2012b)
No voucher	-----	*Myotis nesopolus*	JN20577	Netherlands, Antilles	Bonaire	12.201	-68.26	Larsen *et al.* (2012b)
CM	83427	*Myotis nyctor*	JN020562	Grenada	St. David Parish	----	----	Larsen *et al.* (2012b)
TTU	109225	*Myotis nyctor*	JN020563	Barbados	St. Thomas Parish	13.19	-59.57	Larsen *et al.* (2012b)
TTU	109229	*Myotis nyctor*	JN020565	Barbados	St. Thomas Parish	13.20	-59.53	Larsen *et al.* (2012b)
TTU	109230	*Myotis nyctor*	JN020567	Barbados	St. Thomas Parish	13.14	-59.60	Larsen *et al.* (2012b)
FMNH	129208	*Myotis oxyotus*	AF376865	Perú	Lima	----	----	Ruedi and Mayer (2001)
TTU	35360	*Myotis pilosatibialis*	JX130526	México	San Luis Potosí	22.00	-99.00	Larsen *et al.* (2012a)
TTU	35631	*Myotis pilosatibialis*	JX130518	México	San Luis Potosí	22.00	-99.00	Larsen *et al.* (2012a)
TTU	60981	*Myotis pilosatibialis*	JX130519	San Salvador	Santa Ana	13.46	-88.88	Larsen *et al.* (2012a)
MVZ	226976	*Myotis pilosatibialis*	MW025271	Guatemala	Alta Verapaz	15.61	-90.27	This study
MVZ	226973	*Myotis pilosatibialis*	MW025272	Guatemala	El Quiche	15.46	-90.78	This study
MVZ	224798	*Myotis pilosatibialis*	MW025275	Guatemala	Quetzaltenango	14.74	-91.47	This study
MVZ	AD199	*Myotis riparius*	AF376866	Brazil	Pernambuco	----	----	Ruedi and Mayer (2001)
CM	78651	*Myotis riparius*	JX130490	Venezuela	----	----	----	Larsen *et al.* (2012a)
CM	78659	*Myotis riparius*	JX130474	Venezuela	Bolívar	----	----	Larsen *et al.* (2012a)
TTU	99378	*Myotis riparius*	JX130491	Paraguay	Canindeyú, Paraguarí	-24.46	-54.66	Larsen *et al.* (2012a)
CM	68443	*Myotis riparius*	JX130473	Suriname	Paramaribo	----	----	Larsen *et al.* (2012a)
Voucher 3011	----	*Myotis* cf. *riparius*	AM261891	Costa Rica	La Selva	----	----	Stadelmann *et al.* (2007)
TTU	85344	*Myotis riparius*	JX130469	Ecuador	Esmeraldas	1.23	-78.76	Larsen *et al.* (2012a)
TTU	85345	*Myotis riparius*	JX130515	Ecuador	Esmeraldas	1.23	-78.76	Larsen *et al.* (2012a)
TTU	102883	*Myotis riparius*	JX130492	Ecuador	Esmeraldas	1.09	-78.70	Larsen *et al.* (2012a)
TK	22703	*Myotis riparius*	JX130436	Perú	Huánuco	----	----	Larsen *et al.* (2012a)
THKMys	ET3	*Myotis riparius*	AM262336	Brazil	----	----	----	Stadelmann *et al.* (2007)
TTU	85090	*Myotis riparius*	TK104318	Ecuador	Pastaza	-1.46	-78.10	Larsen *et al.* (2012a)
TTU	122454	*Myotis riparius*	JX130448	Paraguay	Canindeyú	-23.98	-55.36	Larsen *et al.* (2012a)
MVZ	185999	*Myotis ruber*	AF376867	Brazil	Salesopolis	-22.16	-48.75	Ruedi and Mayer (2001)
UAMI	15305	*Myotis velifer*	JX130589	México	Michoacán	----	----	Larsen *et al.* (2012a)
UAMI	15306	*Myotis velifer*	JX130438	México	Michoacán	----	----	Larsen *et al.* (2012a)
MVZ	146766	*Myotis velifer*	AF376870	México	Michoacán	27.06	-109.01	Stadelmann *et al.* (2007)
UAMI	15304	*Myotis velifer*	JX130462	México	Michoacán	----	----	Larsen *et al.* (2012a
TTU	110032	*Myotis velifer*	JX130582	México	Tamaulipas	24.01	-98.34	Larsen *et al.* (2012a)
TTU	44818	*Myotis velifer*	EU680299	México	Tamaulipas	----	----	Parlos *et al.* (2008) Unpublished
TTU	43197	*Myotis velifer*	AY460343	USA	Oklahoma	----	----	Rodriguez and Ammerman (2004)
CS -H	TK 46327	*Myotis velifer*	JX130592	México	Michoacán	----	----	Larsen *et al.* (2012a)
TK	48587	*Myotis velifer*	EF222340	USA	Texas	----	----	Baird *et al.* (2008)
TTU	44816	*Myotis velifer*	JX130478	México	Tamaulipas	----	----	Larsen *et al.* (2012a)
TTU	60983	*Myotis velifer*	JX130477	San Salvador	Santa Ana	----	----	Larsen *et al.* (2012a)
TTU	109261	*Myotis velifer*	JX130468	USA	Texas	29.50	-103.43	Larsen *et al.* (2012a)
No voucher	----	*Myotis vivesi*	AJ504406	México	Gulf of California	28.52	113.02	Stadelmann *et al.* (2004)

MVZ	155853	*Myotis yumanensis*	AF376875	USA	California	38.04	-122.80	Stadelmann *et al.* (2007)
CM	77691	*Myotis* cf. *nigricans*	JX130497	Suriname	Marowijne	----	----	Larsen *et al.* (2012a)
TTU	47514	*Myotis* sp.	JX130449	México	Yucatán	ca.20.96	ca. -89.59	Larsen *et al.* (2012a)
JAG	286	*Myotis* sp.	JX130525	México	Yucatán	----	----	Larsen *et al.* (2012a)
TK	13532	*Myotis* sp.	AF376852	México	Yucatán	----	----	Ruedi and Mayer (2001)
CM	55764	*Myotis* sp.	JX130489	México	Vera Cruz	----	----	Larsen *et al.* (2012a)
MVZ	226977	*Myotis* sp.	MW025270	Guatemala	Alta Verapaz	15.61	-90.27	This study
CM	77705	*Myotis* sp	JX130505	Suriname	Paramaribo	----	----	Larsen *et al.* (2012a)
TTU	61228	*Myotis* sp	JX1304931	Honduras	Valle	13.30	-87.49	Larsen *et al.* (2012a)
TTU	102707	*Myotis* sp	JX130471	Ecuador	Oro	-3.87	-80.09	Larsen *et al.* (2012a)
TTU	46348	*Myotis* sp	JX130481	Perú	Huánuco	----	----	Larsen *et al.* (2012a)
				Outgroups				
NMPPB	916	*Myotis brandtii*	AM261886	Russia	N-W. Russia	----	----	Stadelmann *et al.* (2007)
Mgf	----	*Myotis gracilis*	AB243030	Japan	Hokkaido	----	----	Kawai *et al.* (2006)
MgE	----	*Myotis gracilis*	AB243029	Japan	Hokkaido	----	----	Kawai *et al.* (2006)
OCUMS	5362	*Myotis gracilis*	AB106605	Japan	Hokkaido	----	----	Kawai *et al.* (2003)
KK	0005	*Myotis yanbarensis*	AB106610	Japan	Hokkaido	----	----	Kawai *et al.* (2003)

Appendix 3. List of specimens used in cytochrome oxidase *c* subunit I analyses of Neotropical *Myotis*. Specimens details, localities, and Genbank accession numbers of sampled individuals of Neotropical *Myotis*. Field Museum of Natural History (FMNH); Museum of Vertebrate, Zoology, University of California Berkeley (MVZ); Museum of Southwestern Biology, The University of New Mexico (MSB); Museum of Texas Tech University (TTU and TK); Royal Ontario Museum (ROM); Zoological Museum of Moscow State University (ZMMU).

Institution	Cat. No./Sequence Code	Species	GenBank	Country	Locality	Lat.	Long.	Source
ROM	120231	*Myotis albescens*	HQ545684	Suriname	Sipaliwini	1.94	-56.06	Lim *et al.* (unpubl.)
TTU	85060	*Myotis armiensis* sp. n.	MW042013	Ecuador	Tungurahua	-1.34	-78.2	This study
MSB	262788	*Myotis armiensis* sp. n.	MW042014	Panamá	Las Nubes Ranger Station, Parque Internacional La Amistad	8.89	-82.61	This study
No voucher	Mke140204.2.VS	*Myotis armiensis* sp. n.	KX814396	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.10	-82.96	Chaverri *et al.* (2016)
No voucher	Mke140204.4.VS	*Myotis armiensis* sp. n.	KX814397	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.10	-82.96	Chaverri *et al.* (2016)
No voucher	Mke140204.5.VS	*Myotis armiensis* sp. n.	KX814398	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.10	-82.96	Chaverri *et al.* (2016)
No voucher	Mke140204.8.VS	*Myotis armiensis* sp. n.	KX814399	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.10	-82.96	Chaverri *et al.* (2016)
No voucher	Mke150126.1.VS	*Myotis armiensis* sp. n.	KX814400	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.08	-82.97	Chaverri *et al.* (2016)
No voucher	Mke150201.18.VS	*Myotis armiensis* sp. n.	KX814403	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.11	-82.96	Chaverri *et al.* (2016)
No voucher	Mke140128.1.VS	*Myotis armiensis* sp. n.	KX814393	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.10	-82.96	Chaverri *et al.* (2016)
No voucher	Mke150126.3.VS	*Myotis armiensis* sp. n.	KX814401	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.08	-82.97	Chaverri *et al.* (2016)
No voucher	Mke140129.1.VS	*Myotis armiensis* sp. n.	KX814394	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.08	-82.97	Chaverri *et al.* (2016)
No voucher	Mke140131.3.VS	*Myotis armiensis* sp. n.	KX814395	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.11	-82.96	Chaverri *et al.* (2016)
No voucher	Mke150126.9.VS	*Myotis armiensis* sp. n.	KX814402	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.08	-82.97	Chaverri *et al.* (2016)
ROM	104302	*Myotis armiensis* sp. n.	JF447424	Panamá	Chiriquí	8.87	-82.75	Clare *et al.* (2011)
ROM	97827	*Myotis nigricans*	JQ601557	Guyana	Kuma River	3.26	-59.71	Engstrom *et al.* (unpubl.)
ROM	106737	*Myotis nigricans*	JQ601572	Guyana	Essequibo River	1.58	-58.63	Lim *et al.* (unpubl.)
ROM	106772	*Myotis nigricans*	JQ601574	Guyana	Gunn´s Strip	1.65	-58.63	Lim *et al.* (unpubl.)

ROM	F43329	*Myotis nigricans*	JQ601579	Guyana	Paruima	5.81	-61.06	Lim *et al.* (unpubl.)
ROM	105148	*Myotis nigricans*	JQ601611	Ecuador	Parque Nacional Yasuní	-0.63	-76.45	Engstrom *et al.* (unpubl.)
ROM	118840	*Myotis nigricans*	JQ601620	Ecuador	Orellana	-0.68	-76.43	Reid *et al.* (unpubl.)
ROM	114671	*Myotis nigricans*	JQ601582	Guyana	Mount Ayanganna	5.33	-53.91	Lim *et al.* (unpubl.)
ROM	98018	*Myotis nigricans*	EF080493	Guyana	Potaro-Sirapurini	4.38	-58.37	Clare *et al.* (2007)
ROM	117431	*Myotis nigricans*	EU096808	Suriname	Sipaliwini	4.54	-56.93	Borisenko *et al.* (2008)
No voucher	Mni150205.28.VS	*Myotis nigricans*	KX814404	Costa Rica	Valle del Silencio, Parque Internacional la Amistad	9.13	-82.95	Chaverri *et al.* 2016
FMNH	174938	*Myotis oxyotus*	JN847707	Perú	Cusco, La Esperanza	-13.17	-71.60	Taylor *et al.* (2011)
MVZ	174408	*Myotis oxyotus gardneri*	MW042015	Costa Rica	Refugio Nacional Tapanti, Cartago	9.69	-83.78	This study
No voucher	Mox140201.4.VS	*Myotis oxyotus gardneri*	KX814406	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.11	-82.96	Chaverri *et al.* (2016)
No voucher	Mox140204.6.VS	*Myotis oxyotus gardneri*	KX814409	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.10	-82.96	Chaverri *et al.* (2016)
No voucher	Mox140201.5.VS	*Myotis oxyotus gardneri*	KX814407	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.11	-82.96	Chaverri *et al.* (2016)
No voucher	Mox140131.1.VS	*Myotis oxyotus gardneri*	KX814405	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.11	-82.96	Chaverri *et al.* (2016)
No voucher	Mox140204.1.VS	*Myotis oxyotus gardneri*	KX814408	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.10	-82.96	Chaverri *et al.* (2016)
No voucher	Mox150125.2.VS	*Myotis oxyotus gardneri*	KX814410	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.11	-82.96	Chaverri *et al.* (2016)
No voucher	Mox150125.3.VS	*Myotis oxyotus gardneri*	KX814411	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.11	-82.96	Chaverri *et al.* (2016)
No voucher	Mox150126.10.VS	*Myotis oxyotus gardneri*	KX814412	Costa Rica	Valle del Silencio, Parque Internacional La Amistad	9.11	-82.96	Chaverri *et al.* (2016)
MVZ	226976	*Myotis pilosatibialis*	MW042012	Guatemala	Alta Verapaz	15.61	-90.27	This study
TTU	35360	*Myotis pilosatibialis*	MW042011	México	San Luis Potosí	ca. 22.00	ca. -99.00	This study
ROM	101352	*Myotis pilosatibialis*	JF446523	El Salvador	Santa Ana	14.42	-89.37	Clare *et al.* (2011)
ROM	101433	*Myotis pilosatibialis*	JF446527	El Salvador	Santa Ana	14.42	-89.37	Clare *et al.* (2011)
ROM	101432	*Myotis pilosatibialis*	JF446528	El Salvador	Santa Ana	14.42	-89.37	Clare *et al.* (2011)
ROM	101431	*Myotis pilosatibialis*	JF446529	El Salvador	Santa Ana	14.42	-89.37	Clare *et al.* (2011)
ROM	101357	*Myotis pilosatibialis*	JF446532	El Salvador	Santa Ana	14.42	-89.37	Clare *et al.* (2011)
ROM	101356	*Myotis pilosatibialis*	JF446533	El Salvador	Sant Ana	14.42	-89.37	Clare *et al.* (2011)
ROM	101355	*Myotis pilosatibialis*	JF446535	El Salvador	Sant Ana	14.42	-89.37	Clare *et al.* (2011)
ROM	101354	*Myotis pilosatibialis*	JF446536	El Salvador	Sant Ana	14.42	-89.37	Clare *et al.* (2011)
ROM	116560	*Myotis riparius*	EF080496	Guyana	Potaro-Siparuni	5.25	-59.61	Clare *et al.* (2007)
No voucher	AZ2407	*Myotis velifer*	GU723140	USA	Arizona	----	----	Streicker *et al.* (2010)
ROM	101358	*Myotis velifer*	JF446538	El Salvador	Santa Ana	14.42	-89.37	Clare *et al.* (2011)
No voucher	AZ4490	*Myotis yumanensis*	GU723138	USA	Arizona	----	----	Streicker *et al.* (2010)
No voucher	CA49	*Myotis yumanensis*	GU723137	USA	California	----	----	Streicker *et al.* (2010)
TTU	47514	*Myotis* sp.	MW042010	México	Yucatán	ca. 20.96	ca. -89.59	This study
ROM	99232	*Myotis* sp.	JF446808	Guatemala	Petén	16.30	-89.33	Clare *et al.* (2011)
ROM	99233	*Myotis* sp.	JF446809	Guatemala	Petén	16.30	-89.33	Clare *et al.* (2011)
ROM	96463	*Myotis* sp.	JF447270	México	Yucatán, Loltun	20.25	-89.48	Clare *et al.* (2011)
ROM	FN33842	*Myotis* sp.	JF447274	México	Quintana Roo, Tulum	ca. 20.21	ca. -87.46	Clare *et al.* (2011)
ROM	FN33841	*Myotis* sp.	JF447275	México	Quintana Roo, Tulum	ca. 20.21	ca. -87.46	Clare *et al.* (2011)
			Outgroups					
No voucher	Isolate IN 90	*Myotis lucifugus*	GU723128	USA	Indiana	----	----	Streicker *et al.* (2010)
KZM	SVN 14-08	*Myotis brandtii*	JF4429261	Russia	Sakhalin Region	----	----	Kruskop *et al.* (unpubl.)
ZMMU	SVK 71-08_1	*Myotis brandtii*	JF4429271	Russia	Republic of Gorno-Altay	51.28	84.73	Kruskop *et al.* (unpubl.
ZMMU	SVK 71-08_2	*Myotis brandtii*	JF4429281	Russia	Republic of Gorno-Altay	51.28	84.73	Kruskop *et al.* (unpubl.)
ZMMU	S-171531	*Myotis brandtii*	JF4429291	Russia	Kirov Region	57.35	49.09	Kruskop *et al.* (unpubl.)

Appendix 4. List of taxonomic samples included in nuclear gene analyses of Neotropical *Myotis* with institution, catalog number, species, locality and GenBank accession numbers: American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CM); Field Museum of Natural History (FMNH); Indiana State University Collection (ISUV); Museum of Southwestern Biology, The University of New Mexico (MSB); Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ); Museum of Texas Tech University (TTU and TK); Universidad Autónoma Metropolitana-Iztapalapa (UAMI).

Institution	Cat. No.	Species	Locality	RAG2	PRKC1	STAT5A	THY
CM	77691	*Myotis albescens*	Suriname, Marowijne	GU328076	GU328317	GU328390	GU328460
AMNH	261790	*Myotis albescens*	Bolivia, Beni	MW042018	MW041998	MW041984	MW041970
MSB	262085	*Myotis armiensis* sp. n.	Chiriquí, Panama	MW042027	MW042008	MW041994	MW041980
QCAZ	17245	*Myotis armiensis* sp. n.	Napo, Ecuador	(not sequenced)	MW042005	MW041991	MW041977
MSB	75643	*Myotis auriculus*	New Mexico, USA	MW042019	MW041999	MW041985	MW041971
TK	79325	*Myotis californicus*	USA, Texas	GU328078	GU328319	GU328392	GU328462
TK	83155	*Myotis ciliolabrum*	USA, Texas	GU328080	GU328321	GU328394	GU328464
MSB	43105	*Myotis ciliolabrum*	Mexico, Baja California	MW042016	MW041996	MW041982	MW041968
TTU	31503	*Myotis dominicensis*	Dominica, St. Joseph Parish, Dominica	GU328081	GU328322	GU328395	GU328465
MSB	279297	*Myotis evotis*	USA, New Mexico	MW042020	MW042000	MW041986	MW041972
UAMI-TK	43186	*Myotis fortidens*	Mexico, Michoacán	GU328082	GU328323	GU328396	GU328466
TK	13532	*Myotis* sp.	Yucatán, México	GU328083	GU328324	GU328397	GU328467
FMNH	141600	*Myotis levis*	Sao Paulo, Brazil	GU328085	GU328326	GU328399	GU328469
MSB	70384	*Myotis levis*	Bolivia	MW042021	MW042001	MW041987	MW041973
FMNH	129210	*Myotis nigricans*	Amazonas, Perú	GU328088	GU328329	GU328402	GU328472
AMNH	268591	*Myotis riparius*	Paracou, French Guiana	GU328089	GU328330	GU328403	GU328473
AMNH	268649	*Myotis riparius*	Bolivia, Cochabamba	MW042022	MW042002	MW041988	MW041974
AMNH	261108	*Myotis riparius*	Bolivia, Chuquisaca	MW042024	MW042004	MW041990	MW041976
ISUV 6454 -DWS	6454	*Myotis septentrionalis*	USA, Indiana	GU328090	GU328331	GU328404	GU328474
TTU	79330	*Myotis thysanodes*	USA, Texas	GU328091	(not sequenced)	(not sequenced)	GU328475
TTU	78599	*Myotis velifer*	USA, Texas	AY141033	GU328333	GU328406	GU328476
MSB	53789	*Myotis velifer*	Mexico, Sonora	MW042023	MW042003	MW041989	MW041975
TTU	79545	*Myotis volans*	USA, Texas	GU328092	GU328334	GU328407	GU328477
TTU	43200	*Myotis yumanensis*	USA, Oklahoma	GU328094	GU328336	GU328049	GU328479
MSB	42790	*Myotis* sp.	Mexico, Baja California	MW042028	MW042009	MW041995	MW041981
AMNH	268651	*Myotis keaysi*	Bolivia, Cochabamba	MW042025	MW042006	MW041992	MW041978
MSB	235490	*Myotis* cf. *nigricans*	Bolivia, Tarija	MW042026	MW042007	MW041993	MW041979
				Outgroup			
MSB	94052	*Myotis* cf. *ikonnikovi*	Mongolia, Ovorkhangai	MW042017	MW041997	MW041983	MW041969

Appendix 5. Post-hoc multiple comparison test with Bonferroni corrected approach.

Factor	Group 1	Grupo 2	Sample size group 1	Sample size group 2	Statistics	df	p	p. adj	p. adj. signif
PC1	*M. armiensis* sp. n.	*M.* sp.	10	5	1.5093	12.9886	0.155	0.31	ns
PC1	*M. armiensis* sp. n.	*M. o. gardneri*	10	6	-5.1609	13.8910	0.000148	0.001	**
PC1	*M. armiensis* sp. n.	*M. str. keaysi*	10	5	-4.1027	10.1119	0.002	0.013	*
PC1	*M.* armiensis sp. n.	*M. str. pilosatibialis*	10	8	-1.9745	9.5891	0.078	0.233	ns
PC1	*M.* sp.	*M. o. gardneri*	5	6	-8.5816	8.9647	1.29E-05	0.000129	***
PC1	*M.* sp.	*M. str. keaysi*	5	5	-6.1634	6.4085	0.000651	0.005	**
PC1	*M.* sp.	*M. str. pilosatibialis*	5	8	-5.6729	4.6410	0.003	0.015	*
PC1	*M.* o. *gardneri*	*M. str. keaysi*	6	5	0.0678	6.7613	0.948	0.948	ns
PC1	*M.* o. *gardneri*	*M. str. pilosatibialis*	6	8	6.0262	5.7218	0.001	0.008	**
PC1	M. str. keaysi	*M. str. pilosatibialis*	5	8	3.6629	4.2129	0.02	0.079	ns
PC2	*M. armiensis* sp. n.	*M.* sp.	10	5	7.4576	10.0559	2.10E-05	0.000189	***
PC2	*M. armiensis* sp. n.	*M. o gardneri*	10	6	0.7331	13.5877	0.476	0.476	ns
PC2	*M. armiensis* sp. n.	*M. str. keaysi*	10	5	2.8433	11.4061	0.016	0.062	ns
PC2	*M. armiensis* sp. n.	*M. str. pilosatibialis*	10	8	3.6824	10.5644	0.004	0.019	*
PC2	*M.* sp.	*M. o. gardneri*	5	6	-10.3063	6.5480	2.76E-05	0.000221	***
PC2	*M.* sp.	*M. str. keaysi*	5	5	-9.9125	6.7270	2.95E-05	0.000221	***
PC2	*M.* sp.	*M. str. pilosatibialis*	5	8	-9.9022	10.9032	8.76E-07	8.76E-06	****
PC2	*M. o. gardneri*	*M. str. keaysi*	6	5	3.0094	8.2366	0.016	0.062	ns
PC2	*M. o. gardneri*	*M. str. pilosatibialis*	6	8	4.3703	7.3463	0.003	0.018	*
PC2	*M. str. keaysi*	*M. str. pilosatibialis*	5	8	1.5858	8.3097	0.15	0.3	ns

Appendix 6. Molecular synapomorphies of *Myotis armiensis* sp. n, as revealed by maximum-parsimony (MP) analysis of cytochrome *c* oxidase subunit I (657 bp). Molecular transformations were optimized on a 50 % majority-rule consensus tree of the most parsimonious tree (576 steps; [CI] = 0.429) resulting from the MP analysis of the cytochrome *c* oxidase subunit I matrix. 17 fixed derived characters states were found in the newly identified lineage. Of these, 2 which are indicated by asterisks, have not evolved independently in any other species of New World *Myotis*. The remaining have appeared secondarily in at least one species of New World *Myotis*.

	Nucleotide position /Codon position	Character state in *M. armiensis* sp. n.	Characters Consistency Index
1	3/3	T	0.333
2	93/3	A	0.222
3	93/3	A	0.222
4	102/3	C	0.333
5	162/3	C	0.400
6	180/3	G	0.250
7	264/3	G	0.500
8	366/3	C	0.250
9	375/3	T	0.200
10	427/1	C	0.333
11	447/3	C	0.500
12	477/3	G	0.500
13	507/3	C	0.250
14	594/3	C	0.333
15	641/2*	A	1.000
16	646/1*	A	1.000
17	648/3	G	0.250

Appendix 7. Molecular synapomorphies of *Myotis armiensis* sp. n., as revealed by maximum-parsimony (MP) analysis of partial cytochrome *b* (~ 710 bp). Molecular transformations were optimized on a 50 % majority-rule consensus tree of the most parsimonious tree (2846 steps; [CI] = 0.238) resulting from the MP analysis of partial cytochrome *b*. 31 fixed derived characters states were found in the newly identified lineage. Of these, 1, which is indicated by asterisk, has not evolved independently in any other species of Neotropical *Myotis*. The remaining have appeared secondarily in at least one species of Neotropical *Myotis*.

	Nucleotide position /Codon position	Character state in M. armiensis sp. n.	Characters Consistency Index
1	120/3	T	0.167
2	120/3	C	0.167
3	141/3	G	0.333
4	165/3	C	0.053
5	156/3	G	0.250
6	189/3	T	0.167
7	315/3	A	0.167
8	336/3	T	0.333
9	405/3	G	0.125
10	408/3	C	0.214
11	426/3	A	0.111
12	444/3	T	0.111
13	471/3	C	0.333
14	507/3	C	0.500
15	513/3	C	0.111
16	537/3	C	0.200
17	**570/3***	**G**	**1.000**
18	603/3	T	0.167
19	678/3	C	0.167
20	697/1	T	0.200
21	723/3	C	0.200
22	741/3	C	0.154
23	744/3	T	0.143
24	756/3	C	0.077
25	759/3	C	0.125
26	765/3	C	0.100
27	780/3	C	0.100
28	798/3	C	0.100
29	804/3	C	0.100
30	813/3	G	0.100
31	822/3	T	0.143

Appendix 8. Molecular synapomorphies of *Myotis armiensis* sp. n., as revealed by maximum-parsimony (MP) analysis of protein kinase C, iota (PRKCI, *n* = 402 bp). Molecular transformations were optimized on a 50 % majority-rule consensus tree of the most parsimonious tree (59 steps; [CI] = 0.966) resulting from the MP analysis of protein kinase C, iota. All 4 fixed characters have not evolved independently in any other species of New World *Myotis*.

	Nucleotide position	Character state in M. armiensis sp. n.	Characters Consistency Index
1	29	G	1.000
2	51	C	1.000
3	240	T	1.000
4	371	G	1.000

Appendix 9. Molecular synapomorphies of *Myotis armiensis* sp. n., as revealed by maximum-parsimony (MP) analysis of signal transducer and activator of transcription 5A (STAT5A, *n* = 414 bp). Molecular transformations were optimized on a 50 % majority-rule consensus tree of the most parsimonious tree (134 steps; [CI] = 0.754) resulting from the MP analysis of signal transducer and activator of transcription 5A. 23 fixed derived characters states were found in the newly identified lineage. Of these, 9, which are indicated by asterisk, has not evolved independently in any other species of New World *Myotis*. The remaining have appeared secondarily in at least one species of New World *Myotis*.

	Nucleotide position	Character state in *M. armiensis* sp. n.	Characters Consistency Index
1	10	C	0.500
2	15	C	0.500
3	**18***	**C**	**1.000**
4	**48***	**A**	**1.000**
5	56	C	0.500
6	69	C	0.500
7	72	G	0.667
8	**99***	**C**	**1.000**
9	145	C	0.333
10	148	C	0.500
11	154	A	0.333
12	220	C	0.500
13	254	C	0.500
14	**258***	**C**	**1.000**
15	**269***	**C**	**1.000**
16	273	A	0.500
17	**276***	**C**	**1.000**
18	355	C	0.500
19	376	C	0.333
20	**391***	**T**	**1.000**
21	**393***	**G**	**1.000**
22	398	G	0.500
23	**405***	**G**	**1.000**

Appendix 10. Molecular synapomorphies of *Myotis armiensis* sp. n., as revealed by maximum-parsimony (MP) analysis of thyrotropin (THY, *n* = 475 bp). Molecular transformations were optimized on a 50 % majority-rule consensus tree of the most parsimonious tree (138 steps; [CI] = 0.906) resulting from the MP analysis of thyrotropin. 7 fixed derived characters states were found in the newly identified lineage. Of these, 6, which are indicated by asterisk, have not evolved independently in any other species of New World *Myotis*. Only one has appeared secondarily in at least one species of New World *Myotis*.

	Nucleotide position	Character state in *M. armiensis* sp. n.	Characters Consistency Index
1	**161***	**G**	**1.000**
3	**220***	**G**	**1.000**
2	**235***	**G**	**1.000**
4	**277***	**T**	**1.000**
5	**315***	**C**	**1.000**
6	**350***	**G**	**1.000**
7	373	C	0.500