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Mammals of Yacuri National Park, Loja Province, Ecuador

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Abstract

Yacuri National Park, located on the South American continental divide in Loja Province, Ecuador, was surveyed for mammals during four field trips (2009, 2014, 2015, and 2016). All sampling locations were along the western slope of the Andes (3,077–3,454 m) and included: páramo bogs, primary forests, lower páramo, páramo lagoon, a secondary forest, and a mountain ridge. Sherman traps, pitfall traps, camera traps, and mist nets were used to collect 391 specimens. Twelve species were collected, including *Akodon mollis*, *Thomasomys cinereus* (a new record for Ecuador), *T. caudivarius*, *T. taczanowskii*, *Microryzomys altissimus*, *M. minutus*, *Caenolestes caniventer*, *C. sangay*, *Marmosops caucae*, *Sturnira erythromos*, *Anoura peruana*, and *Sylvilagus andinus*. One additional species, *Pseudalopex culpaeus*, was documented with photography. This study also compares the effects of elevation on Ecuadorean rodent diversity at the taxonomic tribe level. Cytochrome-*b* analysis was conducted on specimens collected in 2016 to confirm identifications and to determine the phylogenetic relationship of each taxon.

Key words: ecology, Ecuador, elevation gradient, mammals, Yacuri National Park

Resumen

El Parque Nacional Yacuri, ubicado en la división continental de Sudamérica en la provincia de Loja, Ecuador, fue encuestado para mamíferos durante cuatro viajes de campo (2009, 2014, 2015 y 2016). Todos los lugares de muestreo se encontraban a lo largo de la vertiente occidental de los Andes (3,077–3,454 m) e incluían: pantanos de páramo, bosques primarios, páramo inferior, laguna páramo, un bosque secundario y una cadena montañosa. Se utilizaron trampas Sherman, trampas de trampas, trampas para cámaras y redes de niebla para recolectar 391 especímenes. Se recolectaron doce especies, incluyendo *Akodon mollis*, *Thomasomys cinereus* (un nuevo registro para Ecuador), *T. caudivarius*, *T. taczanowskii*, *Microryzomys altissimus*, *M. minutus*, *Caenolestes caniventer*, *C. sangay*, *Marmosops caucae*, *Sturnira erythromos*, *Anoura peruana*, y *Sylvilagus andinus*. Una especie adicional, *Pseudalopex culpaeus*, se documentó con fotografía. Este estudio también compara los efectos de la elevación en la diversidad de roedores ecuatorianos a nivel de la tribu taxonómica. El análisis de citocromo-*b* se realizó en los especímenes de 2016 para confirmar las identificaciones y determinar la relación filogenética de cada taxón.

Palabras claves: ecología, Ecuador, gradiente de elevación, mamíferos, Parque Nacional Yacuri

INTRODUCTION

Established in 2009, Yacuri National Park is part of the Podocarpus-El Condor Biosphere Reserve located on the border between the provinces of Loja and Zamora Chinchipe in southern Ecuador along the Peruvian border. The primary habitat mix of the park is southern Andean brush and grassland páramo with patches of high altitude evergreen forests. In addition, the park contains lagoons, streams, and bogs dominated by grasses and mosses. Rocks that surround the bogs support a thick growth of lichens, and the slopes around the bogs typically are dominated by *Polylepis* trees. The areas with human usage generally are comprised of secondary temperate evergreen forests; this is especially true of the area around the visitors' cabin.

The park spans the continental divide and thus contains both Pacific and Atlantic watersheds. The bedrock of the western slope in the park is a complex of andesitic lavas, pyroclastics, shales, and rhyolite. The eastern slope is dominated by schists, quartzites, and gneisses (Longo and Baldock 1982).

Plant taxa and families in the páramo bogs and patch forests include: Poaceae; Asteraceae, *Chuquiraga jussieui*; Apiaceae, *Calceolaria* sp., *Eryngium humile*; Valerianaceae, *Valeriana rigida*; Fabaceae, *Dalea coerulea*; Bromeliaceae, *Tallandsia* sp. and *Puya clava*; Brassicaceae; Rosaceae, *Polylepis hirsute*; Gentianaceae, *Halenia weddelina*; Malvaceae; Lycopodiaceae, *Lycopodium magellanicum*; Blechnaceae; Scrophulariaceae; Plantaginaceae; and Melastomataceae, *Brachyotum jamesonii*.

Herein we report the results of four surveys conducted during 2009, 2014, 2015, and 2016 of small mammals along the western slope in the park, near the continental divide. These surveys ascertain the species of small mammals that occur in Yacuri National Park and provide material to facilitate the understanding of the ecology and biogeography of the mammals of Ecuador.

MATERIALS AND METHODS

Study area and survey sampling.—Yacuri National Park, Loja Province, Ecuador, was surveyed during four years at various sites, elevations, and seasons so as to provide a relatively complete synopsis of the mammal fauna of the park. The initial survey was conducted 9−13 July 2009 at the Laguna Negra (site 10.5, Fig 1). A second survey was conducted 8−11 July 2014 in the páramo grassland. Surveys in 2015 and 2016 sampled the same locations, but in different seasons: 23 April−5 May 2015 and 9 July−28 July 2016. The páramo lagoon, páramo bog, and temperate evergreen forests near the visitors' cabin were the sites most frequently sampled (Fig. 1).

Two hundred Sherman traps were set each trapping session, for a total of 3,800 trap nights. The traps were set in different habitats including streams, stream banks, forest floors, in trees, and along the tree-lined ecotone of bogs. Pitfall traps were set in the páramo lagoon, temperate evergreen forest, and lower páramo along logs and in open areas. Twelve-meter mist nets were set in the temperate evergreen forest across a stream at 3,226 m and in the lower páramo at 3,183 m in a meadow surrounded by trees. Three camera traps were set in ecotone areas between forests and páramo. All voucher specimens (skins, skulls, skeletons, and frozen liver tissue) were deposited in either the Abilene Christian University Natural History Collection (ACUNHC) and/or the Sección Mastozoología, Museo de Zoología (QCAZ) at Pontificia Universidad Católica del Ecuador (PUCE). The guidelines for the treatment of wild animals in research as stated by the American Society of Mammalogists (Sikes et al. 2016) were followed.

To aid in species identification, other researchers (named in the acknowledgments) examined some specimens. The identity of some specimens was further confirmed with sequences from the cytochrome-*b* gene (Cyt*b*). These sequences were compared to GenBank reference specimens that had been identified previously. This study followed the nomenclature of Tirira (2017)

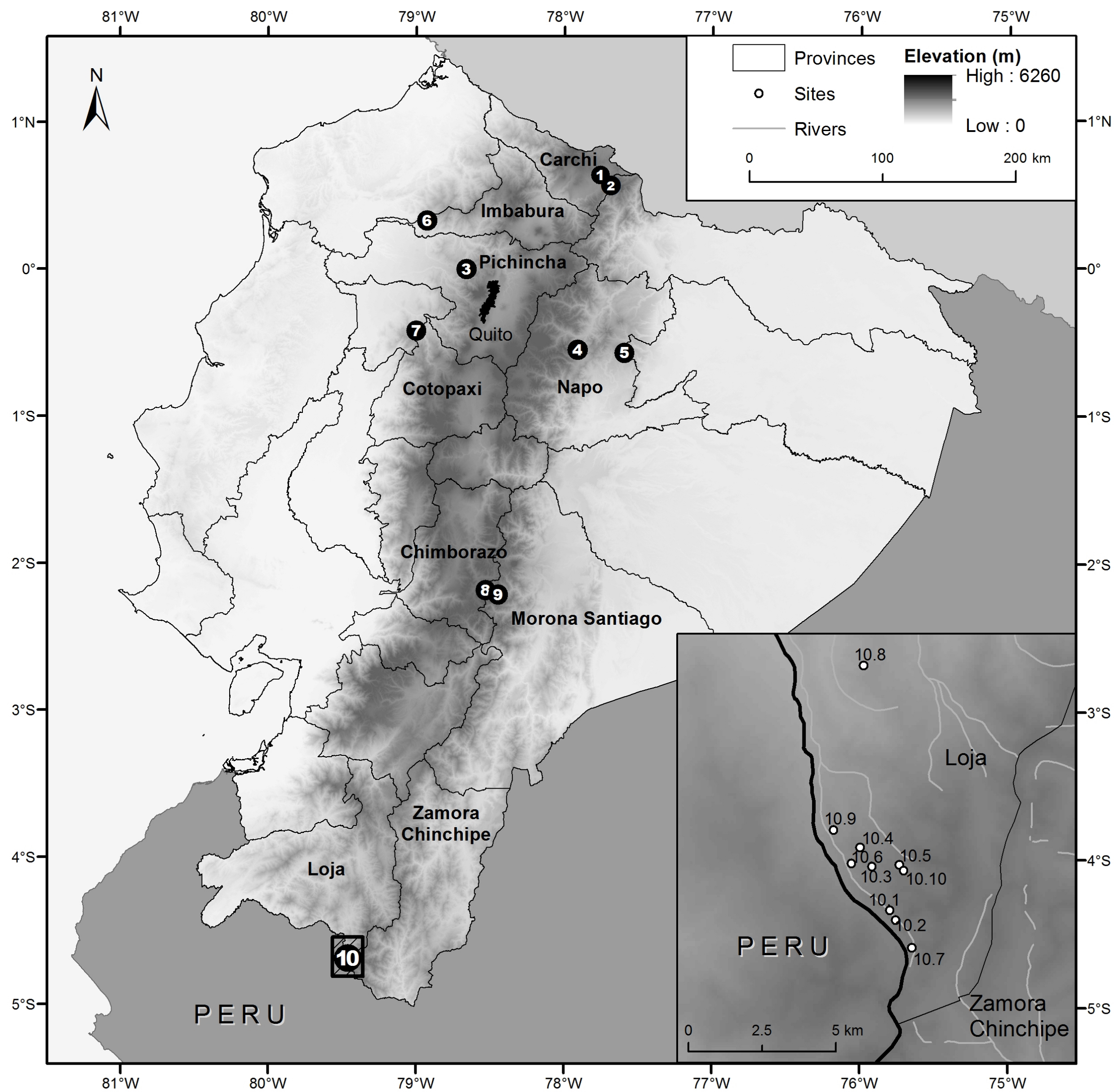

Figure 1. Map of collection locations for this study (area 10) and previous studies (1–9; Lee et al. 2006a, 2006b, 2008, 2010, 2011, 2015) in Ecuador. Inset map shows specific locations for the Yacuri studies reported herein. The 2016 study sites were: the páramo bog 1 (Site 10.1; 4°43'30.88" S, 79°26'04.21" W, 3,393 m); páramo bog 2 (Site 10.2; 4°43'41.60" S, 79°25'57.77" W, 3,422 m); forest near the visitor cabin (Site 10.3; 4°42'42.62" S, 79°26'23.67" W, 3,226 m); lower páramo (Site 10.4; 4°42'21.88" S, 79°26'36.70" W, 3,183 m); páramo Black Lagoon (Site 10.5; 4°42'41.00" S, 79°25'53.88" W, 3,481 m); a secondary forest (Site 10.6; 4°42'39.26" S, 79°26'46.20" W, 3,077 m); and a mountain ridge (Site 10.7; 4°44'11.78" S, 79°25'39.81" W, 3,454 m). In 2009, the survey site was 10.8 (4°39'01.97" S, 79°26'32.82" W, 2,543 m); the 2014 site was 10.9 (4°42' 02.31" S, 79°27'05.82" W, 2,872 m); and the 2015 site was 10.10 (4°42'47.16" S, 79°25'48.94" W, 3,407 m). Previous study sites in Ecuador include: 1 and 2, Guandera; 3, Tandayapa; 4, Cosanga; 5, Vulcan Sumaco; 6, Santa Rosa; 7, Otonga; and 8 and 9, Sangay.

as it reflects the most current taxonomy of Ecuadorean mammals; however, the nomenclature of Pacheco (2015) was followed for *T. cinereus*.

Shannon Index (Shannon 1948) values were calculated and used to generate an ecological comparison of the evenness of diversity with that of other Ecuadorean survey sites (Lee et al. 2006a, 2006b, 2008, 2010, 2011, and 2015). This index assumes that the proportion of individuals indicates their importance to diversity in an area (Shannon 1948). Further, a principal component analysis was conducted on polymorphic samples of *Akodon* from the 2016 survey to uncover any potential trends in morphology that could indicate multiple species being present.

Taxon sampling for DNA extraction and sequencing.—All of the specimens from the 2016 survey were subjected to phylogenetic Cyt*b* analysis to aid identification. Total genomic DNA was isolated using approximately 0.1 g of EtOH-preserved liver tissue with an EZNA Tissue DNA Kit (Omega Bio-Tek, Norcross, Georgia) following the manufacturer's instructions. Following DNA extraction, samples were PCR amplified using primers MVZ05 and MVZ14 (Smith and Patton 1993) modified on the 5' end with an adapter used in downstream reactions (/5AmMC6/gcagtcgaacatgtagctgactcaggtcac and /5AmMC6/tggatcacttgtgcaagcatcacatcgtag for MVZ05 and MV14, respectively). A second reaction was performed using the PacBio Universal barcoding kit (which uses the previously mentioned adapters as priming sites) per manufacturer's protocol to add unique barcodes to each sample. Amplified product was run on a 2% agarose eGel (ThermoFisher, Waltham, Massachusetts) and bands were scored qualitatively. Samples were pooled equimolarly based on qualitative band score into one of four, 94-sample pools. Pools were sequenced on a PacBio Sequel (PacBio Inc., Menlo Park, California) and reads analyzed to generate Complementary Consensus Sequence reads (CCS reads). CCS reads were trimmed to remove primers, then aligned. A 75% consensus sequence was generated from the aligned reads for each sample. These sequences were put in a matrix with sequences for expected genera that were pulled from GenBank (Appendix). This matrix was used to generate a neighbor joining tree for all sequences using Mega 7 (Kumar et al. 2015).

RESULTS

In total, 391 specimens were collected in 2009, 2014, 2015, and 2016. Twelve species were identified. The capture of *Thomasomys cinereus* represented a national record, and *Caenolestes caniventer*, *C. sangay*, *Marmosops caucae*, and *Anoura peruana* specimens represented new range records for Yacuri National Park and/or southern Loja. *Marmosops caucae*, *C. caniventer*, and *T. cinereus* represented new elevation records (Pacheco 2015; Tirira 2017). The phylogenetic Cyt*b* analysis results are shown only for *Thomasomys* (Fig. 2) to illustrate the complicated relationships of our *Thomasomys* specimens. The other taxonomic groups showed expected species associations. Basic morphometric measurements (total length, tail length, hind foot length, ear length, and forearm length; in mm) for all species are shown in Table 1.

ORDER PAUCITUBERCULATA
Family Caenolestidae
***Caenolestes caniventer* Anthony, 1921**
Grey-bellied Shrew-opossum

Three males (QCAZ 16146, 16205, and 16357) and two females (QCAZ 16193 and 16262) were collected at the Black Lagoon in 2016. The morphological identification of this species was confirmed with Cyt*b* sequences. These specimens provide a slight elevation record (3,481 m) and also represent the first specimens from Yacuri National Park (Tirira 2017), although they have been documented nearby in Zamora-Chinchipe Province of Ecuador and in Peru (Timm and Patterson 2007; Tirira 2017).

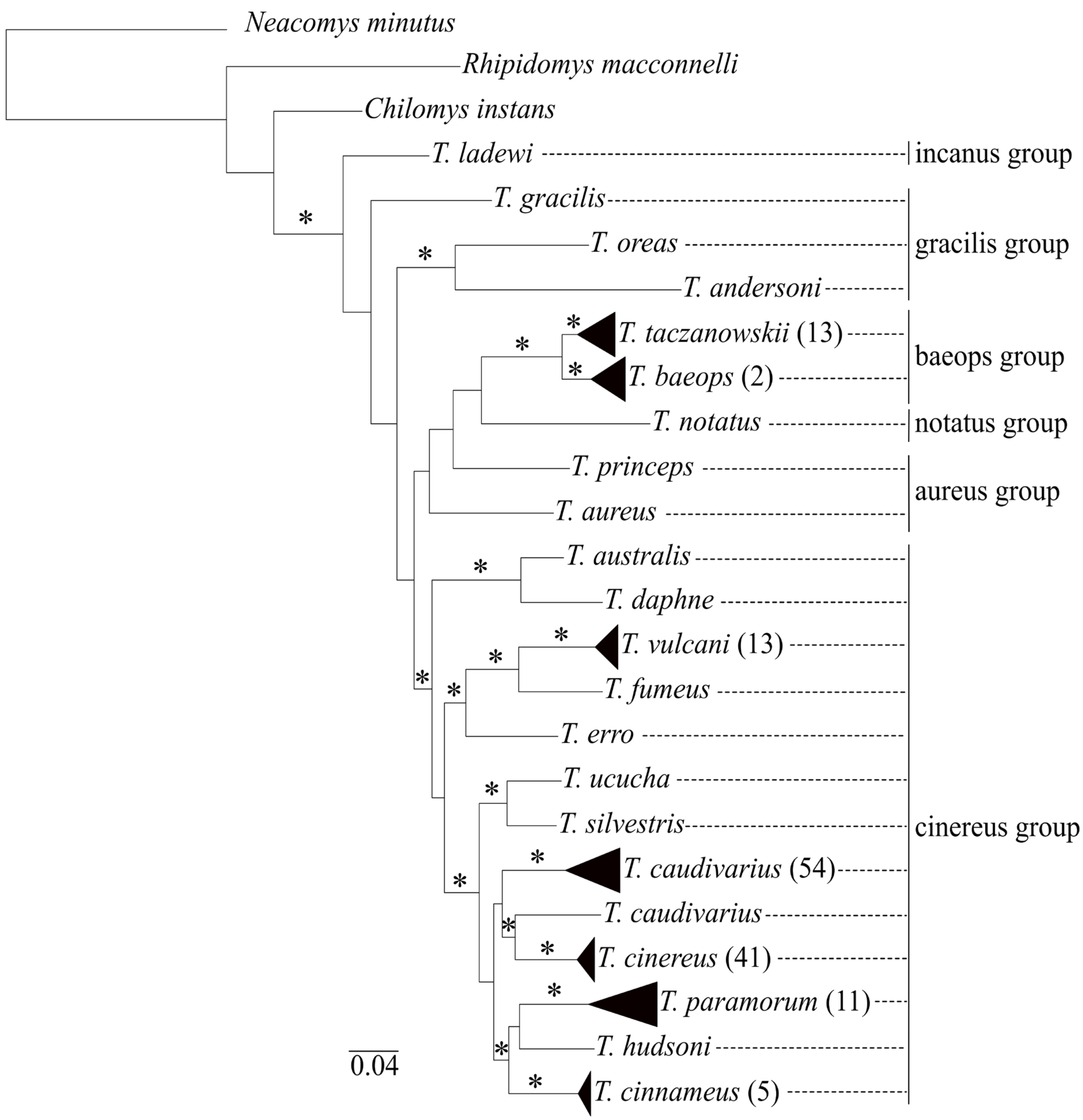

Figure 2. Bayesian analysis of *Thomasomys* Cyt*b* sequences. The tree represents 10 million generations, burnin was set to the first 10% of trees. *Neacomys minutus* was used as an outgroup. Branches with asterisks represent posterior probability scores of ≥ 95%. Numbers in parentheses represent the number of individuals contained in that clade.

Table 1. Range status, collection sites (refer to Fig. 1), and measurements (mm) for all mammal species documented in or near Yacuri National Park, Loja Province, Ecuador. Range designations are as follows: R = major range records (species not previously recorded in Yacuri National Park or within 70 km of the study sites); E = elevation distribution record for the western Ecuadorian Andes; Known = the species had been previously documented by specimens from at or near the location.

Species	Range	Sites	Total length	Tail length	Hind foot length	Ear length	Forearm length
Anoura peruana	R	10.4	74	0	16	16	47
Sturnira erythromos	R	10.4	57–65	0	10–18	14–16	41–42
Microryzomys altissimus	Known	10.1–10.5, 10.8–10.10	146–218	91–126	19–28	10–19	N/A
Microryzomys minutus	Known	10.8	182–194	110–114	19–20	15.1	N/A
Akodon mollis	Known	10.1, 10.3–10.6, 10.8–10.10	103–271	61–160	17–35	11–27	N/A
Thomasomys caudivarius	R	10.1–10.5, 10.10	141–293	118–173	16–32	14–24	N/A
Thomasomys cinereus	R, E	10.1, 10.3–10.5, 10.10	146–309	119–175	20–35	16–22	N/A
Thomasomys taczanowskii	Known	10.1–10.3, 10.9	222–288	126–169	17–32	12–22	N/A
Caenolestes sangay	R	10.10	188–260	101–133	22–25	14–18	N/A
Caenolestes caniventer	R, E	10.5	145–268	129–145	26–28	12–17	N/A
Marmosops caucae	R, E	10.3	215–260	119–140	17–21	15–21	N/A
Sylvilagus brasiliensis	Known	10.4, 10.10	362	40	81	50	N/A
Pseudalopex culpaeus	Known	10.3	N/A	N/A	N/A	N/A	N/A

***Caenolestes sangay* Ojala-Barbour et al., 2013**
Sangay Shrew-opossum

In 2015, 6 females and 7 males (QCAZ 15505−15517) of *C. sangay* were collected in the páramo habitat near lagoons. This species is of medium size with coarse, dark brownish-gray pelage. The canine is hooked near the tip. The incisive foramina are large, and hooked at ends forming closed parentheses; the major palatine foramina are very broad and long compared to those of *C. caniventer*. *Caenolestes sangay* has a narrower, crescent-shaped antorbital vacuity whereas that of *C. caniventer* is always comma-shaped (Ojala-Barbour et al. 2013). These samples provided the first record for the western slope of the Andes and Loja Province.

ORDER DIDELPHIMORPHIA
Family Didelphidae
***Marmosops caucae* (Thomas, 1900)**
Cauca Slender Opossum

One adult female (QCAZ 16261), one juvenile male (QCAZ 16215), and one juvenile female (QCAZ 16236) were collected in 2016 from sites both on the ground and in trees near the visitors' cabin. Although new to Yacuri National Park, the species has been documented in southeastern Loja at Celica (Anthony 1922; Gardner and Creighton 2007). Specimens reported herein represent a major elevation record for the species (3,226 m), as the previously known record high for this species was 2,410 m (Tirira 2017).

ORDER CHIROPTERA
Family Phyllostomidae
***Sturnira erythromos* (Tschudi, 1844)**
Hairy Yellow-shouldered Bat

In 2015, one male (QCAZ 15657) was collected in the lower páramo site; in 2016, two males (QCAZ 16245 and 16344) were collected at that site. The forearm length of each was slightly >42 mm and the body was gray with no shoulder spots. All were collected in a grassy clearing on a steep mountain slope and well within the documented elevation range (Tirira 2017). The identification of this species was confirmed by Cyt*b* data and by comparing these specimens with other *Sturnira* species. *Sturnira erythromos* previously has been reported for Loja Province (Jarrín-V and Clare 2013).

***Anoura peruana* (Tschudi, 1844)**
Peruvian Tailless Bat

One female (QCAZ 16246) was obtained at the lower páramo site in 2016. It was collected at 3,183 m in the same area previously described for the *Sturnira*. It has an incomplete zygomatic arch and the lower first premolar is not blade like. These characters distinguish this species from other *Anoura* in Ecuador (Mantilla-Meluk and Baker 2010). This species was not previously recorded in Yacuri; although there are records for this species in the lowlands, it has a mostly Andean distribution in Ecuador (Tirira 2017).

ORDER CARNIVORA
Family Canidae
***Pseudalopex culpaeus* (Molina, 1782)**
Culpeo

Two foxes were observed and photographed outside the visitors' cabin and in the nearby forest on frequent occasions during the 2016 survey. They were scavenging food that tourists had dropped near the visitors' cabin. Other individuals were seen in the lower páramo and upper páramo at night. This species is found in the Andes in Ecuador and is known to consume rabbits (Novaro 1997).

ORDER LAGOMORPHA
Family Leporidae
***Sylvilagus andinus* (Thomas, 1897)**
Andean Rabbit

One male (QCAZ 15656) was collected in 2015 in a meadow with nearby forest edge. In 2016, rabbits were seen on two occasions on the road from the park to the nearby town of Jimbura (4° 38' 18.24" S, 79° 27' 33.52" W). We also documented rabbits with camera traps in the forest near the park's visitors' cabin. The rabbits were seen at night near cover of thick, low-growing vegetation. The ranges of *S. andinus* and the morphologically similar S. brasiliensis overlap in the park. However, our specimen has short ears, which is characteristic of *S. andinus*, and photographs were taken above 3,000 m, which also is indicative of *S. andinus* (Ruedas et al. 2017; Ruedas pers. com.).

ORDER RODENTIA
Family Cricetidae
***Akodon mollis* Thomas, 1894**
Soft-furred Grass Mouse

In 2009, 27 *A. mollis* (18 females, 8 males, and one sex undetermined; QCAZ 11276−11302) were collected. Six (5 males and 1 female; QCAZ 15114−15116, and 15118−15120) were collected in 2014, and 40 (22 males and 18 females; QCAZ 15519, 15520, 15522−15524, 15526, 15528−15532, 15534, 15536−15538, 15540, 15542, 15544−15549, 15552, 15553, 15555−15561, 15563−15565, 15567, 15573, 15574, 15578, and 15610) were collected in 2015. In 2016, 85 specimens were collected (67 males and 18 females; QCAZ 16145, 16147−16161, 16163, 16166, 16168, 16169, 16174, 16179, 16182, 16185, 16186, 16188, 16189, 16203, 16206, 16212, 16214, 16216, 16220, 16222, 16225, 16226, 16232, 16233, 16240, 16241, 16243, 16244, 16254, 16264−16268, 16270, 16272, 16275−16279, 16281−16290, 16292, 16295, 16297, 16304−16306, 16312, 16319, 16320, 16325, 16326, 16331, 16333, 16338, 16343, 16346, 16348, 16350, 16351, and 16353). Most specimens were collected at one of the páramo bog sites or at the lagoons;

the remainder were obtained in all the other habitats sampled. Most individuals possessed brown pelage but a few had a slight reddish tint along the ventor. There was considerable size variation that was greater than previously reported (Pardiñas et al. 2015). Because of the noticeable morphological variation in the sample, we expected more than one species to be present. Consequently, a principal component analysis was conducted on skull measurements, but the analysis did not show any apparent clustering of samples. Further, an analysis of Cyt*b* sequences confirmed a single species (*A. mollis*) among the 2016 samples. Our study confirms earlier findings, that of a polymorphic species that is common in the grassy habitats of the high Andes (Pardiñas et al. 2015).

Microryzomys altissimus (Osgood, 1933)
Páramo Long-tailed Mouse

Ten specimens, all male (QCAZ 11315−11322, 11325, and 11326) were collected in the 2009 study, 3 (one female and two males; QCAZ 15126−15128) were collected in 2014, and 30 (19 males and 11 females; QCAZ 15579−15596, and 15598−15609) were collected in 2015 near the lagoons. An additional 37 (22 males and 15 females; QCAZ 16165, 16167, 16175, 16177, 16183, 16184, 16187, 16191, 16194, 16200, 16209, 16227−16229, 16239, 16247−16251, 16257−16259, 16280, 16296, 16299−16301, 16303, 16308−16311, 16318, 16322, 16341, and 16352) were collected during the 2016 sampling. Most specimens were collected in the bogs. These specimens are brown dorsally and grayish on the head, with a bicolored tail indicative of *M. altissimus* (Carleton and Musser 1989). Although on some of the specimens these characteristics are harder to distinguish, all have a long incisive foramen that reaches M1, indicative of *M. altissimus* (Carleton 2015). The morphological identification of this species was confirmed with Cyt*b*.

Microryzomys minutus (Tomes, 1860)
Montane Long-tailed Mouse

In 2009, two females (QCAZ 11323 and 11324) were collected. This species is difficult distinguish from its close relative *M. altissimus*. *Microryzomys minutus* often has an ochraceous-tawny pelage and a unicolored tail that is usually longer (110 mm) than in *M. altissimus* (Carleton 2015). Another characteristic of the species is that the incisive foramen is slightly shorter and more ovate than that of *M. altissimus* (Carleton and Musser 1989). *Microryzomys minutus* is broadly distributed in the Andes and has been recorded from 1,030 to 4,000 m, as compared to *M. latissimus*, which tends to occur at elevations higher than 2,800 m (Tirira 2017).

Thomasomys caudivarius Anthony, 1923
White-tipped Andean Mouse

In 2015, 3 females and 4 males (QCAZ 15527, 15625, 15633, 15634, 15641, 15650, and 15654) were collected, and in 2016, 11 males and 8 females (QCAZ 16162, 16178, 16204, 16207, 16211, 16213, 16219, 16235, 16237, 16256, 16269, 16271, 16273, 16274, 16293, 16294, 16307, 16313, and 16321) were collected. The specimens have gray pelage and the tail usually has a white tip. These, and others collected at Sangay National Park, are near the record high elevation for the species of 3,490 m (Lee et al. 2011, 2015; Pacheco 2015; Tirira 2017).

Thomasomys cinereus (Thomas, 1882)
Olive-gray Thomasomys

In 2015, 36 specimens (27 males and 9 females; QCAZ 15611−15624, 15626−15632, 15635−15640, 15642−15645, 15647−15649, 15651, and 15653) were collected. In 2016, 46 specimens (31 males, 14 females, and one unknown; QCAZ 16164, 16170−16173, 16180, 16181, 16192, 16197−16199, 16201, 16202, 16208, 16210, 16221, 16223, 16230, 16231, 16234, 16242, 16253, 16260, 16291, 16314, 16315, 16317, 16323, 16324, 16327−16330, 16332, 16334−16336, 16339, 16340, 16342, 16345, 16347, 16349, and 16354−16356) of *T. cinereus* were obtained. The animals were collected from the following habitats: 14 at the páramo lagoons, 16 in the lower páramo, 12 in the forest near the cabin, and 4 in other habitats. The pelage is uniformly slate gray, with a small white patch of fur in the auricular region. Some specimens also had larger patches of white on their head or neck. The alisphenoid strut is present in most specimens but varies in width and is absent in others (e.g., specimens QCAZ 16354 and QCAZ 16355 had no alisphenoid strut). The morphological identification of this species was confirmed with Cyt*b* data. These are the first confirmed records of the species for Ecuador, although the species is known from locations in nearby Peru. These specimens represent a slight elevation record as well. The previous record was 3,100 m (Pacheco 2015), whereas most of our specimens were collected at the páramo lagoons at 3,481 m. This species has probably been present in Ecuador, as the habitat on both sides of the border is very similar. However, the establishment of the park has provided more opportunities for focused collecting which most likely is the reason for the new record.

Thomasomys taczanowskii **(Thomas, 1882)**
Taczanowski's Andean Mouse

In 2014, two males (QCAZ 15135 and 15139) were collected in trees in the patches of forest, and another male (QCAZ15646) was caught in 2015 in trees in the same habitat. Fifteen specimens (11 males and 4 females; QCAZ 16176, 16190, 16195, 16196, 16217, 16218, 16224, 16238, 16252, 16255, 16263, 16298, 16302, 16316, and 16337) of T. taczanowskii were collected in forests in 2016. The color of all of the specimens is gray. These specimens were near the highest elevation documented in Ecuador (3,400 m) (Lee et al. 2011, 2015; Tirira 2017). Specimens identified as T. taczanowskii clustered with other specimens assigned to this species in the Cyt*b* analysis and confirm the morphological identification.

DISCUSSION

It has been proposed that sigmodontinae genera arrived in the northern Andes from Central America as the techtonic uplift began in the Miocene (Leite et al. 2014). The uplift increased the heterogeneity of habitats and in turn favored the diversification of mountain rodent lineages (Leite et al. 2014). Previous studies of certain non-volant mammals (Patterson et al. 1989; McCain 2005; Wen et al. 2014; Lee et al. 2015) and of bats (Patterson et al. 1996) suggested that the diversity of such mammals is higher at mid-elevation and decreases with increasing elevation (Lee et al. 2015). However, in other taxonomic groups, such as cricetid rodents, the diversity increases at higher elevations. In our study, rodent diversity did not decrease with increasing elevation and the Shannon values did not show a trend for rodents with increasing elevation (Table 2). Other studies (Lee et al. 2006a, 2006b, 2008, 2010, 2011, 2015; Tirira and Boada 2009) have found that when the species richness of different tribes of rodents was compared with the elevation of the study site, the cricetid tribe Thomasomyini became the most dominant group above 2,500 m (Table 2 and Fig. 3). Below 2,500 m, the cricetid tribe Oryzomyini was the dominant group. These patterns were observed in all the years of this study (Table 2) and may account for the high diversity of rodents collected in this study versus that of other taxonomic groups (Miranda et al. 2008). The Shannon values depict an expected trend in bats of decreasing diversity with increasing elevation and no trend in non-volant mammals (Table 2). Other bat genera such as *Myotis* and *Histiotis* that were collected at similar elevations on previous trips were not found, possibly because there were noticeably few flying insects. In addition, high winds may have made the environment too difficult for bats to fly in and the nets easy to detect and avoid.

These collections from Yacuri National Park are part of a broader sampling effort in Ecuador. Six previous studies (Lee et al. 2006a, 2006b, 2008, 2010, 2011, 2015) have examined other areas of primarily montane Ecuador. All of the studies used the same techniques and trapping equipment, and were conducted during the same seasons. Of the other six comparison studies, Yacuri is most similar to Sangay National Park. Both studies were conducted at about 3,400 m in elevation, had similar wet bog habitats, and yielded a high number of *Akodon*. In this study, more specimens of the tribe Akodontini (158) were collected than Thomasomyine rodents (126). However, the diversity of the tribes was different as only one species of Akodontini was collected compared to the three species of Thomasomyini. The number and species of bats collected on this trip was the lowest when compared to the numbers in the other studies (Table 2), likely due to the high elevation and high winds.

Table 2. Past and current survey locations in Ecuador arranged by elevation. The table shows the Shannon values and direct count values for bats, rodents, and total mammals for each location.

Location	Site Number (see Fig. 1)	Elevation	Bat species recorded	H^P for bats	Rodents species recorded	H^P for rodents	Total mammal species recorded	H^P for mammals
Santa Rosa (Lee et al. 2010)	6	450 m	16	1.1	5	0.61	23	1.23
Santa Rosa (Lee et al. 2010)	6	702 m	10	0.86	4	0.60	15	1.03
Santa Rosa (Lee et al. 2010)	6	450–702 m	22	1.19	8	0.79	32	1.31
Otonga (Jarrín and Fonseca 2001)	7	1,300–2,300 m	18	1.02	N/A	N/A	N/A	N/A
Tandayapa (Lee et al. 2006a)	3	1,500–2,000 m	13	0.88	3	0.23	19	0.99
Guajalito (Jarrín and Fonseca 2001)	Not shown	1,800–2,000 m	16	1.03	N/A	N/A	N/A	N/A
Cosanga (Lee et al. 2006b)	4	1,900–2,100 m	15	0.82	3	0.12	20	0.91
Otonga (Lee et al. not published)	7	2,072 m	8	0.83	7	0.34	20	0.75
Volcan Sumaco (Lee et al. 2008)	5	2,500 m	8	0.58	4	0.48	12	0.84
Sangay National Park (Lee et al. 2011)	9	2,962 m	4	0.50	5	0.67	10	0.84
Sangay National Park (Lee et al. 2011)	8	3,400 m	0	N/A	8	0.66	10	0.75
Sangay National Park (Lee et al. 2011)	8 and 9	2,962–3,400 m	4	0.50	8	0.73	15	0.88
Guandera Biological Reserve (Tirira and Boada 2009)	1 and 2	3,340–3,650 m	7	0.76	6	0.61	14	0.99
Guandera Biological Reserve (Lee et al. 2015)	1 and 2	3,340–3,650 m	3	0.26	9	1.07	14	1.15
Yacuri National Park (2016 study)	10	3,077–3,454m	2	0.28	5	0.62	9	0.76
Yacuri National Park (all studies)	10	2,543–3,454m	2	0.24	7	0.63	13	0.69

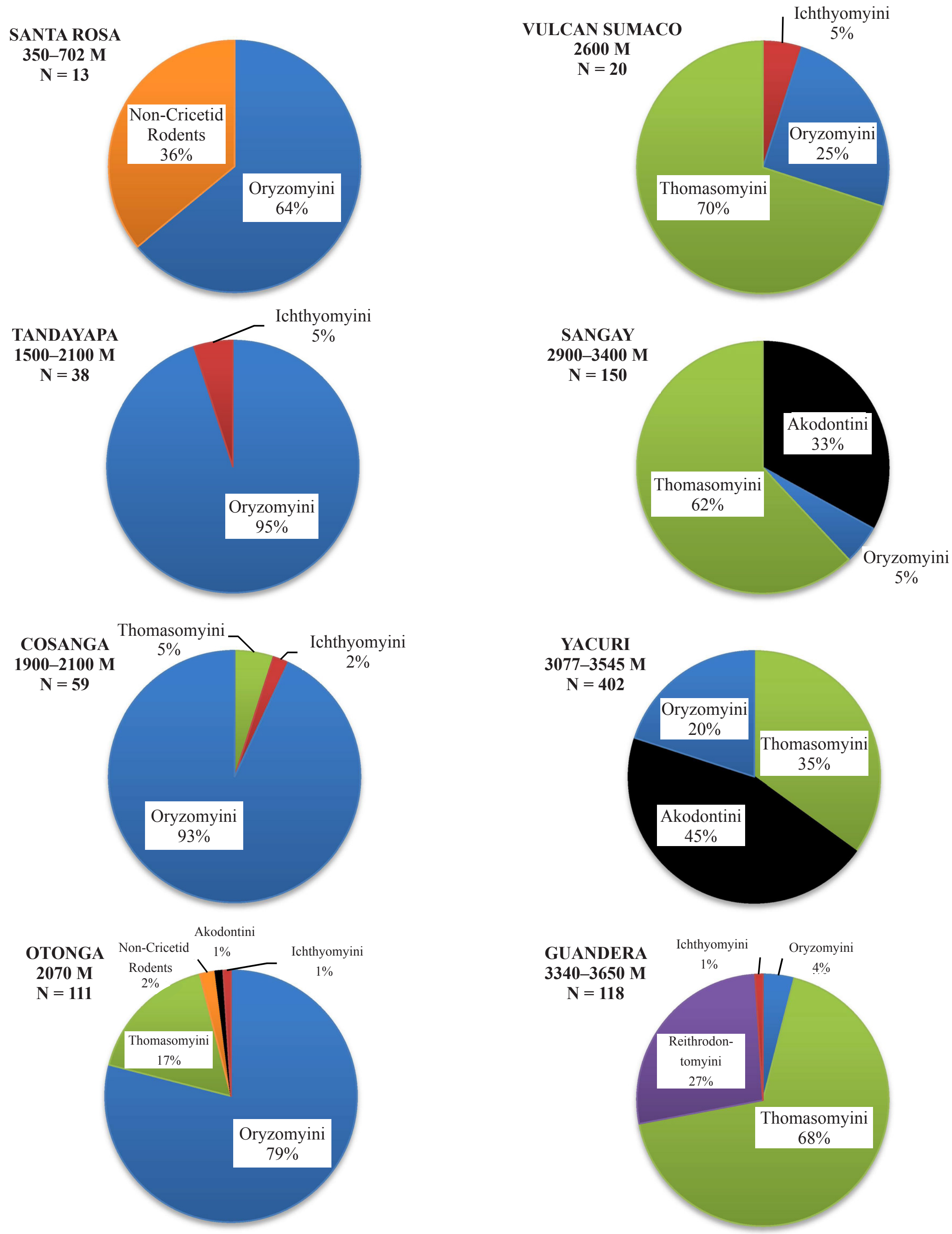

Figure 3. Comparative ecological sample data of cricetid rodents from eight locations surveyed in Ecuador. The pie charts are arranged from lowest to highest elevation, and each chart is arranged at the taxonomic level of cricetid tribe. For this comparison, we used only the 2016 data from Yacuri so as to keep the sampling effort similar to that of all the other studies shown in the diagram. The names in this figure can be cross-referenced with the map (Fig. 1) as follows: 1 and 2 Guandera, 3 Tandayapa, 4 Cosanga, 5 Vulcan Sumaco, 6 Santa Rosa, 7 Otonga, 8 and 9 Sangay, and 10 Yacuri.

All four sampling efforts at Yacuri National Park (2009, 2014, 2015, and 2016) recorded similar species. All of these collections were conducted in the month of July except for the 2015 study, which was conducted from late April to the beginning of May. In Loja, the months of April and May generally have higher precipitation and temperatures than July (Worldweatheronline.com 2018). Even though this effort occurred during the wet season, it still produced a similar proportion of species as compared to the other efforts. For example, *Akodon* was the most common genus recorded, with *Thomasomys* and *Microryzomys* being the next most common in all four years.

Our Cyt*b* analysis of *Caenolestes* supported a sister taxa relationship between *C. caniventer* and *C. sangay*, as also shown by Ojala-Barbour et al (2013). Further, these specimens were consistent with the morphological characters of *C. caniventer* and *C. sangay*. Additional analysis of this group is warranted, because the presence of other cryptic species is possible.

Our phylogenetic analysis of *Thomasomys* depicts expected monophyletic groups of specimens assigned to *T. cinnameus*, *T. cinereus*, *T. vulcani*, *T. taczanowskii*, and *T. caudivarius* (Fig. 2). A specimen of *Chilomys* instans taken in the Guandera Biological Reserve (Lee et al. 2015) and included in the Cyt*b* analysis was recovered in a basal position to the clade containing the *Thomasomys* specimens. However, *Chilomys* was sister to the *Thomasomys* taxa, whereas *Rhipidomys* was basal for the Andean thomasomyine clade.

With the addition of the Yacuri *Thomasomys* species to the Cyt*b* analysis, some sister taxa relationships changed from those of earlier analyses (Lee et al. 2011, 2015). However, others relationships were similar, such as *T. fumeus* being sister to *T. vulcani* (Lee et al. 2015). This relationship agreed with what had been inferred on the basis of morphology by Voss (2003). In the current study, a sister taxa relationship was found by using both Cyt*b* and morphology. The closest relative of *T. taczanowskii* is found to be *T. baeops*, supporting relationships based on morphology concerning the close phylogenetic relationship of these two species (Fig 2).

Sequence analysis of *T. caudivarius* from Yacuri and a specimen from Sangay National Park suggested the presence of more than one species in this group (Fig. 2). Further analysis utilizing additional specimens of *T. caudivarius* will be necessary to determine the taxonomic status of members of this group.

Pacheco (2015) recognized seven species groups within the genus *Thomasomys*. Our analysis of Cyt*b* shows that, with some exceptions, these groups form monophyletic clusters (Fig. 2). The cluster containing all the taxa indicated the cinereus group is monophyletic. However, there appear to be multiple reciprocally monophyletic species groups contained within the cinereus group, which should be investigated further. The baeops group also forms a monophyletic cluster. However, the aureus group members (*T. aureus* and *T. princeps*) were not monophyletic. The aureus species group needs to be investigated further to determine its validity. This pattern also was observed with the *gracilis* group, as *T. gracilis* did not form a monophyletic cluster with the other *gracilis* members, *T. andersoni* and *T. oreas* (Fig. 2). COI gene analysis shows a similar tree topology and relationships among *Thomasomys* species to those obtained from the Cyt*b* data (Pinto et al. 2018), indicating that these relationships are conserved among mitochondrial genes. *Thomasomys* requires additional investigation for a better understanding of the relationships within this group.

With the exception of *P. culpaeus*, larger mammals of conservation concern were not observed in Yacuri National Park during this survey. Yacuri faces threats from roadways and cattle in the area. The road going through the park is not well maintained and erosion of the road is occurring in many areas, which poses a hazard to both people and animals (in the form of vehicle mortality). Cattle ranches are common in the area, especially across the border in Peru. The cattle are not fenced and are free to roam in the park and this has led to overgrazing and habitat destruction. Therefore, fencing that keeps cattle out and allows wildlife to pass through is warranted.

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APPENDIX

List of specimens used as reference sequences in Cyt*b* analyses. Names in parenthesis in the species column represent misidentifications of GenBank names. The comparison groups were analyzed independently from other reference groups.

GenBank	Species	Comparison Group
DQ444329	*Bibimys labiosus*	*Akodon*
AY196165	*Akodon spegazzinii*	*Akodon*
AY702964	*Akodon azarae*	*Akodon*
AY702966	*Akodon philipmyersi*	*Akodon*
EU251018	*Akodon montensis*	*Akodon*
EU260477	*Akodon dayi*	*Akodon*
EU260478	*Akodon varius*	*Akodon*
EU260482	*Akodon simulator*	*Akodon*

GenBank	Species	Comparison Group
EU260484	*Akodon glaucinus*	*Akodon*
EU260487	*Akodon tartareus*	*Akodon*
EU579471	*Akodon paranaensis*	*Akodon*
HM106360	*Marmosa mexicana*	Marsupials
HM106364	*Marmosa robinsoni*	Marsupials
HM106366	*Marmosa rubra*	Marsupials
HM106376	*Marmosa lepida*	Marsupials
HM106401	*Marmosa murina*	Marsupials
AF102816	*Caenolestes fuliginosus*	Marsupials
KF418780	*Caenolestes caniventer*	Marsupials
KF418781	*Caenolestes sangay*	Marsupials
KF418782	*Caenolestes convelatus*	Marsupials
KJ129895	*Didelphis marsupialis*	Marsupials
U34681	*Lestoros inca*	Marsupials
DQ000483	*Peromyscus leucopus*	*Reithrodontomys*
HQ269736	*Peromyscus mexicanus*	*Reithrodontomys*
JX910118	*Peromyscus mexicanus*	*Reithrodontomys*
AF176250	*Reithrodontomys montanus*	*Reithrodontomys*
AF176251	*Reithrodontomys zacatecae*	*Reithrodontomys*
AF176255	*Reithrodontomys raviventris*	*Reithrodontomys*
AY293816	*Reithrodontomys bakeri*	*Reithrodontomys*
AY859429	*Reithrodontomys creper*	*Reithrodontomys*
AY859461	*Reithrodontomys microdon*	*Reithrodontomys*
AY859462	*Reithrodontomys spectabilis*	*Reithrodontomys*
AY859463	*Reithrodontomys tenuirostris*	*Reithrodontomys*
AY859464	*Reithrodontomys chrysopsis*	*Reithrodontomys*
AY859466	*Reithrodontomys hirsutus*	*Reithrodontomys*
AY859467	*Reithrodontomys humulis*	*Reithrodontomys*
AY859470	*Reithrodontomys raviventris*	*Reithrodontomys*
EF990017	*Reithrodontomys brevirostris*	*Reithrodontomys*
EF990021	*Reithrodontomys spectabilis*	*Reithrodontomys*
HQ269729	*Reithrodontomys sumichrasti*	*Reithrodontomys*
HQ269730	*Reithrodontomys fulvescens*	*Reithrodontomys*
HQ269732	*Reithrodontomys megalotis*	*Reithrodontomys*
HQ269734	*Reithrodontomys mexicanus*	*Reithrodontomys*
AF108698	*Mircroryzomys minutus*	*Microryzomys*
EU258535	*Mircroryzomys minutus*	*Microryzomys*

GenBank	Species	Comparison Group
EU579502	*Neacomys* (*Microryzomys*) *minutus*	*Microryzomys*
EU258536	*Neacomys minutus*	*Microryzomys*
EU579503	*Neacomys musseri*	*Microryzomys*
EU579504	*Neacomys spinosus*	*Microryzomys*
KP778425	*Neacomys paracou*	*Microryzomys*
FJ589715	*Carollia perspicillata*	*Sturnira*
KC753786	*Sturnira bogotensis*	*Sturnira*
KC753791	*Sturnira erythromos*	*Sturnira*
KC753813	*Sturnira luisi*	*Sturnira*
KC753818	*Sturnira magna*	*Sturnira*
KC753824	*Sturnira mordax*	*Sturnira*
KC753825	*Sturnira hondurensis*	*Sturnira*
KC753854	*Sturnira oporaphilum*	*Sturnira*
KC753886	*Sturnira lilium*	*Sturnira*
KC753893	*Sturnira tildae*	*Sturnira*
MF441751	*Sturnira* sp.	*Sturnira*
MF441763	*Sturnira luisi*	*Sturnira*
MF441924	*Sturnira parvidens*	*Sturnira*
AF108681	*Rhipidomys macconnelli*	*Thomasomys*
AF108673	*Thomasomys daphne*	*Thomasomys*
AF108674	*Thomasomys gracilis*	*Thomasomys*
AF108675	*Thomasomys ischyurus* (*taczanowskii*)	*Thomasomys*
AF108676	*Thomasomys notatus*	*Thomasomys*
AF108677	*Thomasomys oreas*	*Thomasomys*
DQ914644	*Thomasomys andersoni*	*Thomasomys*
DQ914646	*Thomasomys cinnameus* (*hudsoni*)	*Thomasomys*
DQ914652	*Thomasomys ladewi*	*Thomasomys*
DQ914645	*Thomasomys australis*	*Thomasomys*
DQ914654	*Thomasomys baeops*	*Thomasomys*
EU579476	*Thomasomys erro*	*Thomasomys*
KR818897	*Thomasomys cinnameus*	*Thomasomys*
KR818888	*Thomasomys caudivarius*	*Thomasomys*
KR818899	*Thomasomys ucucha*	*Thomasomys*
KR818900	*Thomasomys silvestris*	*Thomasomys*
KR818901	*Thomasomys fumeus*	*Thomasomys*
KR818905	*Thomasomys princeps*	*Thomasomys*
U03540	*Thomasomys aureus*	*Thomasomys*

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