Mammalia æquatorialis 2023(5): 31–47 ISSN 2697-3286

Mammalia æquatorialis
The Ecuadorian Journal of Mammalogy

Submitted: 2023-02-08 Accepted: 2023-06-21 Published: 2023-12-01
DOI: https://doi.org/10.59763/mam.aeq.v5i.58

ORIGINAL ARTICLE

Mammals of the Tapichalaca Reserve, Zamora Chinchipe, Ecuador

Mamíferos de la Reserva Tapichalaca, Zamora Chinchipe, Ecuador

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ABSTRACT

For some years now, researchers from Abilene Christian University and the Museo de Zoología of the Pontificia Universidad Católica del Ecuador have carried out systematic field studies focused on characterizing the diversity of small mammals in different areas of the Andes mountains of Ecuador. In 2021, we surveyed the mammalian diversity of the Tapichalaca Reserve in Zamora Chinchipe Province, Ecuador. The habitat corresponds to the mountain cloud forest of the eastern Andes. The steep mountain slopes and high rainfall in this habitat cause frequent landslides that result in dense secondary growth forests. The reserve was established to protect the Jocotoco Antpitta (Passeriformes: Grallariidae, *Grallaria ridgelyi*) that is only known from Tapichalaca and a few other nearby mountain forests. The mammalian species we registered were *Didelphis pernigra*, *Marmosops caucae*, *Caenolestes condorensis*, *Syntheosciurus granatensis*, *Oreoryzomys balneator*, *Akodon aerosus*, *Nephelomys albigularis*, *Thomasomys aureus*, *T. caudivarius*, *T. fumeus*, *T. taczanowskii*, *Cuniculus*

Citation:
Lee Jr., T. E., Tinoco N., Jasper, J. G., Camacho, M. A., & Burneo, S. F. (2023). Mammals of the Tapichalaca Reserve, Zamora Chinchipe, Ecuador. *Mammalia aequatorialis*, *5*, 31–47.

Journal homepage: https://mammalia-aequatorialis.org
Asociación Ecuatoriana de Mastozoología

tazanowskii, *Coendou rufescens*, *Anoura geoffroyi*, *Sturnira bidens*, *S. erythromos*, *Myotis oxyotus*, *Leopardus tigrinus* and *Nasua olivacea*.

Keywords: Andes, camera-trapping, diversity, inventory, small mammals.

RESUMEN

Desde hace algunos años, investigadores de Abilene Christian University y del Museo de Zoología de la Pontificia Universidad Católica del Ecuador hemos realizado estudios de campo sistemáticos enfocados en caracterizar la diversidad de pequeños mamíferos en distintas zonas de la Cordillera de los Andes del Ecuador. En 2021 estudiamos la diversidad de mamíferos de la Reserva Tapichalaca, en la provincia de Zamora Chinchipe, Ecuador. El hábitat corresponde a bosque nublado de los Andes orientales. Las empinadas laderas de las montañas y las altas precipitaciones en este hábitat provocan frecuentes deslizamientos de tierra que dan como resultado densos bosques secundarios. La reserva fue establecida para la protección de la gralaria de Jocotoco (Passeriformes: Grallariidae, *Grallaria ridgelyi*) que solo se conoce de Tapichalaca y algunos otros bosques de montanos cercanos. Las especies de mamíferos registradas fueron: *Didelphis pernigra*, *Marmosops caucae*, *Caenolestes condorensis*, *Syntheosciurus granatensis*, *Oreoryzomys balneator*, *Akodon aerosus*, *Nephelomys albigularis*, *Thomasomys aureus*, *T. caudivarius*, *T. fumeus*, *T. taczanowskii*, *Cuniculus tazanowskii*, *Coendou rufescens*, *Anoura geoffroyi*, *Sturnira bidens*, *S. erythromos*, *Myotis oxyotus*, *Leopardus tigrinus* y *Nasua olivacea*.

Palabras clave: Andes, diversidad, fototrampeo, inventario, pequeños mamíferos.

INTRODUCTION

The forests of the Andes Mountains, along the mid-elevations of the eastern and western slopes, constitute a biodiversity hotspot (Myers et al., 2000), characterized by a high number of species and endemics of some groups of fauna. Among them, small non-volant mammals are a key focus for research due to their remarkable diversity and, generally, limited geographic ranges (do Prado et al., 2015). However, our understanding of this diversity remains incomplete, as indicated by the discovery of new taxa in recent years (Maestri & Patterson, 2016).

The Tapichalaca Reserve is located in the southern Ecuadorean province of Zamora-Chinchipe. This survey is part of an ongoing effort to discover information regarding the natural history, distribution, and ecology of mammals living in the Ecuadorean Andes. Since 2003, a team of scientists from Abilene Christian University and the Museo de Zoología of the Pontificia Universidad Católica del Ecuador have surveyed different sites in the Ecuadorean Andes, following standardized methodology, to characterize the mammalian fauna, especially small non-volant species. Figure 1 shows the localities visited so far, with their respective highest elevations:

- Tandayapa Valley (Pichincha, 2000 m; Lee et al., 2006a),
- Cosanga River Drainage (Napo, 2100 m; Lee et al., 2006b),
- Volcán Sumaco (Sucumbíos, 2500 m; Lee et al., 2008),
- Santa Rosa de Naranjal (Imbabura, 450 m; Lee et al., 2010),
- Sangay National Park (Chimborazo and Morona Santiago, 3400 m; Lee et al., 2011),
- Guandera Biological Reserve (Carchi; 3400 m; Lee et al., 2015),
- Yacuri National Park (Loja, 3450 m, Lee et al., 2018),
- Quimsacocha National Recreation Area (Azuay, 3860 m, Lee et al., 2021a), and,
- Otonga Forest Reserve (Cotopaxi, 2300 m; Lee et al., 2021b).

The purpose of this study was to report on the mammalian diversity of the Tapichalaca Reserve and compare our findings with previous studies in other mid- and high-elevation localities in Ecuador.

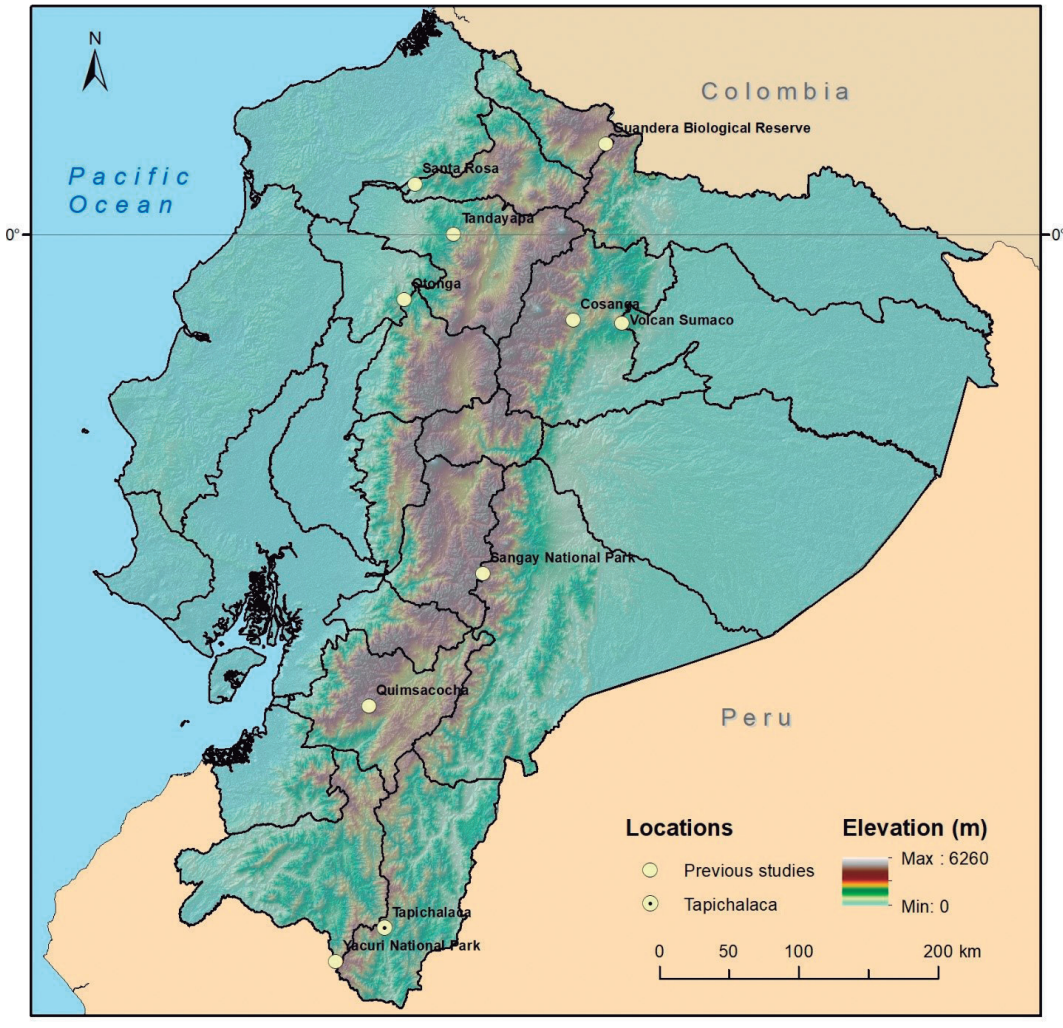

FIGURE 1. Location of Tapichalaca in relation to localities of previous studies.

METHODS

STUDY AREA

The habitat corresponds to a mountain cloud forest of the eastern Andes (coordinates 04°29'31.90" S, 79°07'38.99" W, 2522 m) (Figure 1). According to Tirira (2017), the area is characterized by eastern temperate forests, and the main ecosystem present is the "Southern montane evergreen forest of the Eastern Andes Mountain Range" (BsMn02, Báez et al., 2013). The area has an average annual temperature of 15.7 °C (Hijmans et al., 2005).

The study site is geologically composed of schists, quartzites, and gneisses (Longo & Baldock, 1982). The geology and climate directly impact the soil type, affecting the types of plants that can grow in the area and thus the overall ecology. Moreover, the geophysical structure (steep mountain slopes) and high rainfall (2500 to 3000 mm per year, 10 to 20 °C) provide conditions for frequent landslides (World Weather Online, 2018). Landslides set the successional clock back, creating a patchwork of secondary forests. Some of the patches we encountered were in early-stage succession, with bare ground visible and only sparsely vegetated. Oth-

er sections of the patches caused by the same landslide had dense stands of bamboo.

Tapichalaca has dense stands of forest. The trees are usually covered in mosses, ferns, and epiphytic vascular plants. Streamside vegetation includes halloid liverworts. There are thick stands of bamboo (Poaceae). *Lycopodium* is common on the forest floor, and upland open areas usually had lichens and mosses. Plants we identified include: Onagraceae (*Fuchsia* sp.), Polypodiaceae (ferns), Melastomataceae, Campanulaceae (*Centropogon* sp.), Bromeliaceae (*Tillandsia* sp.), Orchidaceae, Araceae, Arecaceae (palms), Violaceae (*Viola* sp.), Asteraceae, Cyatheaceae (tree ferns), Gunneraceae (Gunnera sp.) (MAE, 2013; Patzelt, 2012).

Field work

We surveyed the mammals of Tapichalaca Reserve from 3 July to 24 July 2021. We installed seven Browning Strike Force (model BTC-5HDE) trail cameras along the forest trails for 21 consecutive nights. Outside the trails, the vegetation is too dense to walk through. Digital images were taken with a Canon 5D Mark III camera for all the species recorded.

We set 204 Sherman traps to capture small terrestrial mammals and five Tomahawk traps for medium-sized mammals over 21 nights (for a cumulative effort of 4389 trap-nights); four 9-m mist nets were used to capture bats over the same period (189 net-nights). In addition, some bats of the genus *Anoura* were captured with the use of a butterfly net.

All our voucher specimens, including skins, skulls, skeletons, parasites, and frozen liver tissue, were deposited in the Abilene Christian University Natural History Collection (ACUN-HC) and in the Sección de Mastozoología del Museo de Zoología (QCAZ-M) at the Pontificia Universidad Católica del Ecuador.

Specimen identification

To aid in our identification of Thomasomys, DNA was extracted from tissue samples from the specimens in the collections of the ACUN-HC. We ran a PCR of each sample for the mitochondrial gene COI. The COI gene was sequenced at Azenta Corporation. We then used Sequencher® to analyze the sequences and check for patterns of similarity within *T. fumeus*, *T. vulcani*, and other *Thomasomys species*. Using the results from Sequencher, we constructed a maximum likelihood bootstrap phylogenetic tree, treating each codon position as a separate partition. The maximum likelihood was selected as a result of 1000 replicated searches. The results were assessed by nonparametric bootstrapping and Bayesian posterior probabilities.

We analyzed the geographic distribution of Cricetid rodent tribes using a classical cluster analysis, with a Euclidean similarity index based on standardized data, conducted in PAST v4.12 (Hammer et al., 2001). We changed the original percentage data to log transformation for standardization. For nomenclature and taxonomic order, we followed Burgin et al. (2020a, b). Even though many other studies with similar goals have been carried out in the Ecuadorian Andes (Anthony, 1922; Barnett, 1999; Brito & Ojala-Barbour, 2016; Curay et al., 2019, 2022; Jarrín-V., 2001; Jarrín-V. & Fonseca, 2001; Ojala-Barbour et al., 2019; Pilatasig, 2022; Tirira & Boada, 2009; Voss, 2003), we decided to use only the inventories previously developed by the same team of scientists so the comparisons could be made with a standardized sampling effort.

RESULTS

We collected 169 specimens from 19 species; six of these taxa were documented using photography only (only species with photos of sufficient quality to ensure an unequivocal taxonomic ID are reported). These species represent five mammalian orders and ten families.

Species accounts

Order Didelphimorphia
Family Didelphidae

Didelphis pernigra J. A. Allen, 1900 (Appendix B:a): This species was only detected using trail cameras. It was the most commonly pho-

tographed animal. White head with black mask that starts at the nose and continues past the eyes; triangular stripe in the center of the forehead (Astúa, 2015), recognizable by the white ears and black and white contrasting facial markings (Tirira, 2017).

Marmosops caucae (Thomas, 1900) (Appendix A:a): We collected 15 individuals, eight males and seven females (QCAZ 18936–18950). These specimens are characterized by a dark coloration around the eye. Dorsal fur grayish-brown to brown with uniform gray underparts, ventral fur either light gray or with patches of white in the gular and genital regions. No postorbital process on the skull, nasal bones expanded in the maxilo-frontal suture, palatine fenestrae present, subsquamosal foramen constricted antero-posteriorly, C1 without accessory cusps (Diaz-Nieto et al., 2011). Tail longer than the head and body. Measurements (in mm): total length 246–310, tail length 146–183, hind foot length 18–23, ear length 18–21.

Order Paucituberculata
Family Caenolestidae

Caenolestes condorensis Albuja and Patterson, 1996 (Appendix A:b): We collected 11 specimens (QCAZ 18916–18926), six males and five females. One of the females had two embryos, one in each uterus. Many of these specimens were obtained by setting traps in a small shed. The shed was used to store wooden boards and logs. Some of these specimens, likely juveniles because of their smaller size, conform morphologically to *C. convelatus* (medium size and contrasting ventral fur) while three specimens conform to C. condorensis (large size and ventral fur color that does not contrast with the dorsum) (Ojala-Barbour et al., 2013). Phylogenetic analysis of the COI gene reveals that these specimens form a distinct clade from either *C. convelatus* or *C. sangay* and are monophyletic. The COI sequences for these specimens are nearly identical to each other, indicating that they are part of the same population. Therefore, our assumption is that these specimens are all *C. condorensis*, based on the characteristics of the larger (adult) individuals. Measurements (in mm): total length 237–284, tail length 118–146, hind foot length 24–30, ear length 13–16.

Order Rodentia
Family Sciuridae

Syntheosciurus granatensis (Humboldt, 1811) (Appendix B:d): We obtained two out-of-focus images on a trail camera of S. granatensis. Taxonomy follows De Abreu-Junior et al. (2020), acknowledging that further research is needed into the taxonomic status of Neotropical squirrels, but Tirira et al. (2022) accepted the genus name. No specimens were collected, and none were observed directly.

Family Cricetidae

Akodon aerosus Thomas, 1913 (Appendix A:c): Thirty-seven specimens (QCAZ 18875–18911) were collected (21 males and 16 females). These specimens are very dark in color when compared with *A. mollis* specimens, which is consistent with published descriptions (Tirira, 2017). Skull strongly-built, with broad interorbital region, rostrum short and broad; smooth and non-beaded supraorbital ridges, anterior edges of zygomatic plates straight to slightly concave; incisive foramina long and wide, broad mesopterygoid fossa (Thomas, 1913). One female had two embryos. Measurements (in mm): total length 162–197, tail length 75–100, hind foot length 12–18, ear length 12–18.

Nephelomys albigularis (Tomes, 1860) (Appendix A:d): We collected 23 specimens (12 males and 11 females, QCAZ 18928–18935, 18955–18969). One female had two embryos. Rostrum slightly narrow, nasolacrimal capsules inflated, interorbital region narrow, hourglass-shaped, and without ridges, zygomatics arches are convergent and narrow, incisive foramen is short with slightly broad, mesopterigoid fossa present with anterior margin rounded or V-shaped, without postpalatal processes (Ruelas et al., 2021). The presence or absence of an alisphenoid strut is variable in these specimens; they have an anterior median flexus. Measurements (in mm):

total length 207–341, tail length 113–191, hind foot length 31–37, ear length 17–23.

Oreoryzomys balneator (Thomas, 1900) (Appendix A:e): Thirty-five specimens were collected of this species (QCAZ 18973–19007). There were 23 males and 12 females in this sample, and four females had embryos; three had two embryos and one had three. Very small and delicate skull, rostrum long and narrow, flanked by small and discrete nasolacrimal foramina, zygomatic arches slightly divergent posteriorly, jugals absent, interorbital region is antero-posteriorly short, wide, and hourglass-shaped, rounded anterior border of mesopterygoid fossa, alisphenoid strut absent; stapedial foramen and sphenofrontal foramen present, configuring carotid circulatory pattern 1 (Percequillo et al., 2015). Measurements (in mm): total length 175–223, tail length 98–132, hind foot length 18–30, ear length 14–18.

Thomasomys aureus (Tomes, 1860; Appendix A:f): Six individuals were collected (two males and four females; QCAZ 19018–19023). This is one of the largest species within the genus *Thomasomys* (head body length 154–159 mm). Braincase moderately broad and not inflated, incisive foramina long and moderately narrow, usually extending posteriorly between molar anterocones. Palatal bridge short and narrow with maxillary palatal pits present. Auditory bullae small and uninflated, mesopterygoid fossa broad and somewhat parallel-sided, carotid circulatory pattern derived (stapedial foramen small, internal squamosal-alisphenoid groove absent, sphenofrontal foramen absent; Pacheco, 2015). The dorsal fur is orange/brown with dark gray underfur. Measurements (in mm): total length 367–405, tail length 213–242, hind foot length 34–39, ear length 20–24.

Thomasomys caudivarius Anthony, 1923 (Appendix A:g): Twenty-one individuals were captured (13 males and 8 females; QCAZ 19028–19048). Skull moderately long, interorbital region moderately broad and hourglass-shaped, oval incisive foramina, more contracted anteriorly, and moderately long, mesopterygoid fossa broad with subparallel margins, carotid circulatory pattern primitive (stapedial foramen present, squamosal alisphenoid groove and sphenofrontal foramen present; Pacheco, 2015). These specimens have a white-tipped tail and are a medium-sized group of *Thomasomys*. Measurements (in mm): total length 232–300, tail length 139–186, hind foot length 26–32, ear length 16–21.

Thomasomys fumeus Anthony, 1924: Three males were collected (QCAZ 19025–19027). Dorsal fur has a brownish wash; lighter (than the dorsum) brown wash on ventral fur. Short skull with moderately broad rostrum, interorbital region moderately broad and hourglass-shaped with rounded margins, zygomatic plates narrow, zygomatic arches moderately convergent anteriorly, incisive foramina wide with contracted anterior and posterior margins, mesopterygoid fossa broad, wider anteriorly and convergent posteriorly. Carotid circulatory pattern primitive (Pacheco, 2015; Brito & Arguero, 2016). This is the southernmost record for *T. fumeus* by 264 km from the previous record (Brito & Arguero, 2016). Measurements (in mm): total length 257–271, tail length 126–137, hind foot length 29–31, ear length 18–20.

Thomasomys taczanowskii (Thomas, 1882) (Appendix A:h): Four individuals were collected (QCAZ 18970, 19024, 19049, 19050) (three males and one female). These specimens are similar in appearance in fur color to *Thomasomys paramorum*; however, skull morphology differs. Short and delicate rostrum, short nasals, interorbital region narrow with faintly marked edges, zygomatic arches narrow and converging anteriorly, incisive foramina narrow and long extending backward between anterior borders of M1s. Carotid circulatory pattern derived (Pacheco, 2015). Measurements (in mm): total length 207–248, tail length 124–138, hind foot length 25, ear length 13–16.

Family Erethizontidae

Coendou rufescens (Gray, 1865) (Appendix B:b): We captured an individual with a butter-

fly net, photographed it, and released it after identification. A few of the quills that the individual shed were collected (QCAZ 18927). Long dorsal fur absent and only spikes present; most spikes tricolored (with brownish or reddish tips), defensive spikes on rump and base of tail bicolored; bristle-spikes absent (Voss, 2015).

Family Cuniculidae

Cuniculus taczanowskii (Stolzmann, 1885) (Appendix B:c): Images of *C. taczanowskii* were captured with a trail camera set up to face a compost pile at night. This animal had rows of spots along the dorsum. This pattern differentiates *C. taczanowskii* from *C. paca*. Furthermore, it would be unusual to find *C. paca* above 2000 m altitude.

Order Chiroptera

Family Phyllostomidae

Anoura geoffroyi Gray, 1838 (Appendix C:a,b): We observed about 60–100 individuals of *Anoura* feeding at hummingbird feeders on most nights. We obtained four specimens (one male and three females; QCAZ 18912–18915) using a handheld butterfly net. Dorsal fur presents a silvery gray coloration on the sides of the neck and shoulders; ears short and rounded. Tail absent, short calcar, and caudal membrane reduced and hairy. Zygomatic arches incomplete, lower jaw protrudes well beyond the upper lip. Measurements (in mm): total length 63–70, hind foot length 9–16, ear length 10–12, forearm 42.5–43.7.

Sturnira bidens Thomas, 1915 (Appendix C:c): Five specimens were collected (two males and three females; QCAZ 19008–19012). All these bats had two lower incisors; this character differentiates this species from the others (with the exception of *S. nana*, which has a pair of tiny, spiculated external lower incisors, and is much smaller than *S. bidens*; Gardner, 2008). Measurements (in mm): total length 65–70, hind foot length 14–17, ear length 12–16, forearm 42.3–45.0.

Sturnira erythromos (Tschudi, 1844) (Appendix C:d): Five specimens were collected (one male and four females; QCAZ 19013–19017). Small, with an elongated rostrum, upper central incisors projecting anteriorly and spaced at the tip; lower central incisors bilobed. Mandibular molars have poorly defined lingual-sided cusps, giving each molar a continuous, flat appearance (Gardner, 2008). Measurements (in mm): total length 63–68, hind foot length 13–16, ear length 12–14, forearm 40.5–44.5.

Family Vespertilionidae

Myotis oxyotus (W. Peters, 1866) (Appendix C:e, f): Three specimens were collected (QCAZ 18951–18953) (two males and one female). These bats were seen on the eaves of the house in which we were staying. We obtained our specimens using mist nets. The dorsal fur on these specimens is dark brown with yellow tips. Basic measurements (in mm): total length 90–95, tail length 38–41, hind foot length 9–10, ear length 13–15, forearm 39.3–40.2.

Order Carnivora

Family Felidae

Leopardus tigrinus (Schreber, 1775) (Appendix B:e): Two cameras set along trails captured images of a cat; the combination of a short, many-banded tail and a short face are indicative of *L. tigrinus* (Roland Kays, pers. comm.).

Family Procyonidae

Nasua olivacea Gray, 1866 (Appendix B:f): One individual was captured in a Tomahawk trap. This individual had thick dark brown pelage with a light gray-brown underfur on the dorsum. The head had a dark mid-dorsum stripe that covered the rostrum and narrowed to a midpoint between the ears. The tail was bushy, and the dorsal fur was dark gray with blackish tips; the ventral fur was light brown. We took blood samples (QCAZ 18954), photographs, and released the individual. This species was formerly designated as *Nasuella olivacea* but recently reclassified as *Nasua* (Ruiz-García et al., 2021).

DISCUSSION

The Tapichalaca Reserve was established to protect the endangered Jocotoco Antpitta (*Grallaria ridgelyi*) that we observed. The Jocotoco Antpitta's known range is limited to a few small areas of mountain cloud forests near Mount Tapichalaca, Ecuador. and nearby northern Peru (Del Hoyo & Collar, 2016). The forest preserved for the Jocotoco Antpitta has become an important refuge for other forest-dependent species, such as small and medium-sized mammals, such as the ones we reported here.

The mammal species diversity we encountered is similar to a number of cloud forests areas that have been previously surveyed. These areas include Otonga and Guandera; in comparison, both had similar species diversity of *Anoura*, *Sturnira*, *Thomasomys*, and *Nephelomys* (Lee et al., 2015, 2021b). The vegetation in all three locations was indicative of high mountain temperate cloud forests.

The rodent data (Cricetidae: Sigmodontinae) were compared with past studies with similar sampling efforts that were conducted in different areas of Ecuador (Table 1, Figure 1).

Table 1. Elevation and latitudinal distribution of the tribes of the rodent subfamily Sigmodontinae. Survey locations in Ecuador arranged by elevation.

Location	Elevation range (m)	Latitude (degrees)	Thomasomyini	Oryzomyini	Akodontini	Ichthyomyini	Reithrodontomyini	Phyllotini	Sigmodontini
Santa Rosa de Naranjal (Lee et al., 2010)	450–700	0.3308	0	100%	0	0	0	0	0
Tandayapa (Lee et al., 2006a)	1500–2000	0.0036	0	95%	0	5%	0	0	0
Cosanga (Lee et al., 2006b)	1900–2100	-0.5500	5%	93%	0	2%	0	0	0
Otonga (Lee et al., 2021b)	1300–2300	-0.4197	19%	80%	0	1%	0	0	0
Volcan Sumaco (Lee et al., 2008)	2400-2500	-0.5719	70%	25%	0	5%	0	0	0
Tapichalaca (Lee et al., this study)	2500-2550	-4.4922	27%	43%	30%	0	0	0	0
Sangay National Park (Lee et al., 2011)	2900-3400	-2.1933	59%	5.6%	35.4%	0	0	0	0
Guandera Biological Reserve (Lee et al., 2015)	2960–3400	0.5892	68%	4%	0	1%	27%	0	0
Yacuri National Park (Lee et al., 2018)	3080–34545	-4.7118	35%	20%	45%	0	0	0	0
Quimsacocha (Lee et al., 2021a)	3570–3865	-3.0542	0	26%	61%	0	0	11.3%	1.1%

Cluster analysis shows more similarity using latitude as a predictor rather than elevation in the way localities are arranged by tribe composition (Figure 2).

When a comparison is made with other sites, Tapichalaca Reserve does present some differences from trends seen at other sites where a similar collecting effort was made. Tapichalaca presents a lower abundance of Thomasomyini as a percentage of the Sigmodontinae rodents that were captured when compared with other sites of similar elevation, such as Volcan Sumaco, Sangay, and Guandera (Table 1). Therefore, Tapichalaca does not show the trend of increasing Thomasomyini numbers and decreasing Oryzomyini numbers with increasing elevation in forested habitats. There is a possibility that Thomasomys numbers are low due to wide fluctuations in rodent numbers from year to year (Lee et al., 2015). This taxonomic/ecological

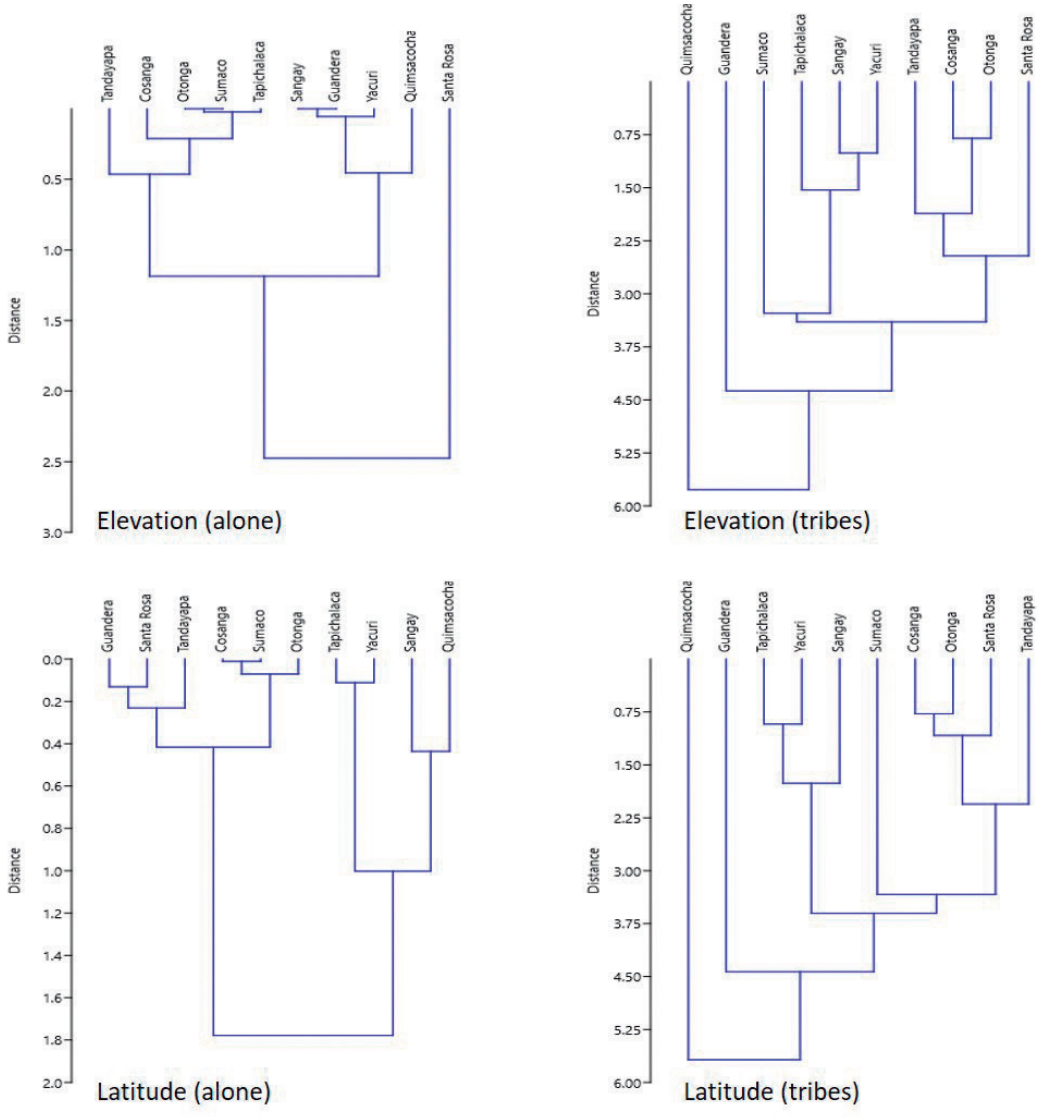

FIGURE 2. Clustering analysis of sampling localities where similar efforts have been made (Table 1). Left: clusters formed by using only elevation (top) and latitude (bottom). Right: clusters formed by using tribe similarity percentages combined with elevation (top) or latitude (bottom).

trend does not hold for paramo locations of Yacuri and Quimsacocha because Akodontini and high-elevation Oryzomyini become more common in this habitat (Table 1).

The abundance of rodent tribes is not only related to elevation, as it may seem intuitively, but also to latitude and even to the side of the Andes on which these populations are located. All these factors affect the dispersal capabilities of small mammals (Brown, 2001). In terms of the connectivity of topography, according to a cluster analysis of the information provided in Table 1, latitude of occurrence explains the similarities of groups assembled by tribe better than elevation (Figure 2), with exceptions made in cases of locations on different slopes of the Andes. Clusters like Tandayapa, Cosanga, Otonga, Santa Rosa and Sumaco, are clustered together by latitude (northern localities, between -0.57 to 0.33 degrees) more closely than when combined by tribe similarity percentages, except for Guanderas, which has a noticeably higher elevation. A similar pattern occurs with southern localities like Tapichalaca, Yacuri, Quinsacocha, and Sangay (-4.71 to -2.19 degrees).

Bat diversity and numbers were similar to other Andean forest sites. For example, *Sturnira bidens*, *S. erythromos*, *Anoura geoffroyi*, and *Myotis oxyotus* are commonly encountered in habitats above 1500 m (Lee et al., 2006a; 2006b; 2008; 2010; 2011; 2015; 2018; 2021a; 2021b). These four species were the only bat species we encountered during the Tapichalaca survey. Bats that are found at high elevations tend to occur over a wide elevation distribution (Patterson et al., 1996). The four species that we found on this survey are most likely habitat generalists and therefore able to survive across a wide range of mountain ecological and vegetation zones (Lee et al., 2018).

There are several conservation concerns regarding the mammals of Tapichalaca. Some of the species we encountered at Tapichalaca were either categorized as IUCN Vulnerable or Near Threatened. For example, *Leopardus tigrinus* and *Caenolestes condorensis* are considered as Vulnerable per the IUCN Red List, both globally and according to the *Red List for Ecuadorian Mammals* (Tirira, 2021). *Nasua olivacea* and *Cuniculus taczanowskii* are listed as Vulnerable on the Ecuadorian Red List and Near Threatened globally. *Nephelomys albigularis* and *Thomasomys caudivarius* are listed as Vulnerable on the Ecuadorian list. *Oreoryzomys balneator* is listed as Data Deficient globally and Near Threatened on the Ecuadorian list. *Thomasomys taczanowskii*, *T. fumeus*, and *Coendou rufescens* are listed as Near Threatened on the Ecuadorian list (Tirira, 2021).

Our camera traps captured a domestic dog feeding at the reserves compost pile. The dog was photographed in the same place as the *C. taczanowskii* and, on occasion, *D. pernigra*. A domestic dog can be a threat to a wide variety of wildlife (Zapata Ríos & Branch, 2018). In addition, agricultural areas can be found all around the reserve, which means that the forests have been removed and that these areas are under grazing pressure.

CONCLUSIONS

With the addition of our specimens and photographic data from Tapichalaca Reserve, we can present a finer-grained picture of the biogeography of the Andean mammals of Ecuador when compared with previous studies. Furthermore, these data highlight the complex biogeographic context in which the mammals of the Andes of Ecuador find themselves. The mammals have had to adapt to the tectonic plate, climatic, and ecological history of the Andes. Hopefully, they will continue to persist and adapt in the face of increasing anthropogenic pressure.

Acknowledgements: We thank the Fundación Jocotoco for its support of this research and for allowing us to use the Tapichalaca Research Station facilities; we also thank the park rangers and staff of the Tapichalaca Reserve for their help in the field. We thank Anita Pilatasig and Johana López from QCAZ-M for their help in preparing and organizing the specimens collected in the field. The collection was done under the Framework Contract for Access to Genetic Resources (No. MAAE-DBI-CM-2021-0165) and the Guía de movilización (No. 00164 Cod. MAAE-CMARG-2021-0260) issued by the Ministerio del Ambiente, Agua y Transición

Ecológica. Pebbles Lee read earlier versions of this manuscript.

Authors' contributions: TEL and NT completed fieldwork and ran taxonomical analyses on the specimens; TEL drafted the manuscript; MAC curated, catalogued, and accessed specimens in the QCAZ mammal collection; SFB facilitated fieldwork, procured all necessary permits for research, collection, and export, developed the geographical analysis, and drafted and formatted the manuscript.

Conflict of interest: The authors declare that we have no conflict of interest.

Funding: This study was funded by the Clark Stevens Endowed Professorship. Field work was supported by Pontificia Universidad Católica del Ecuador.

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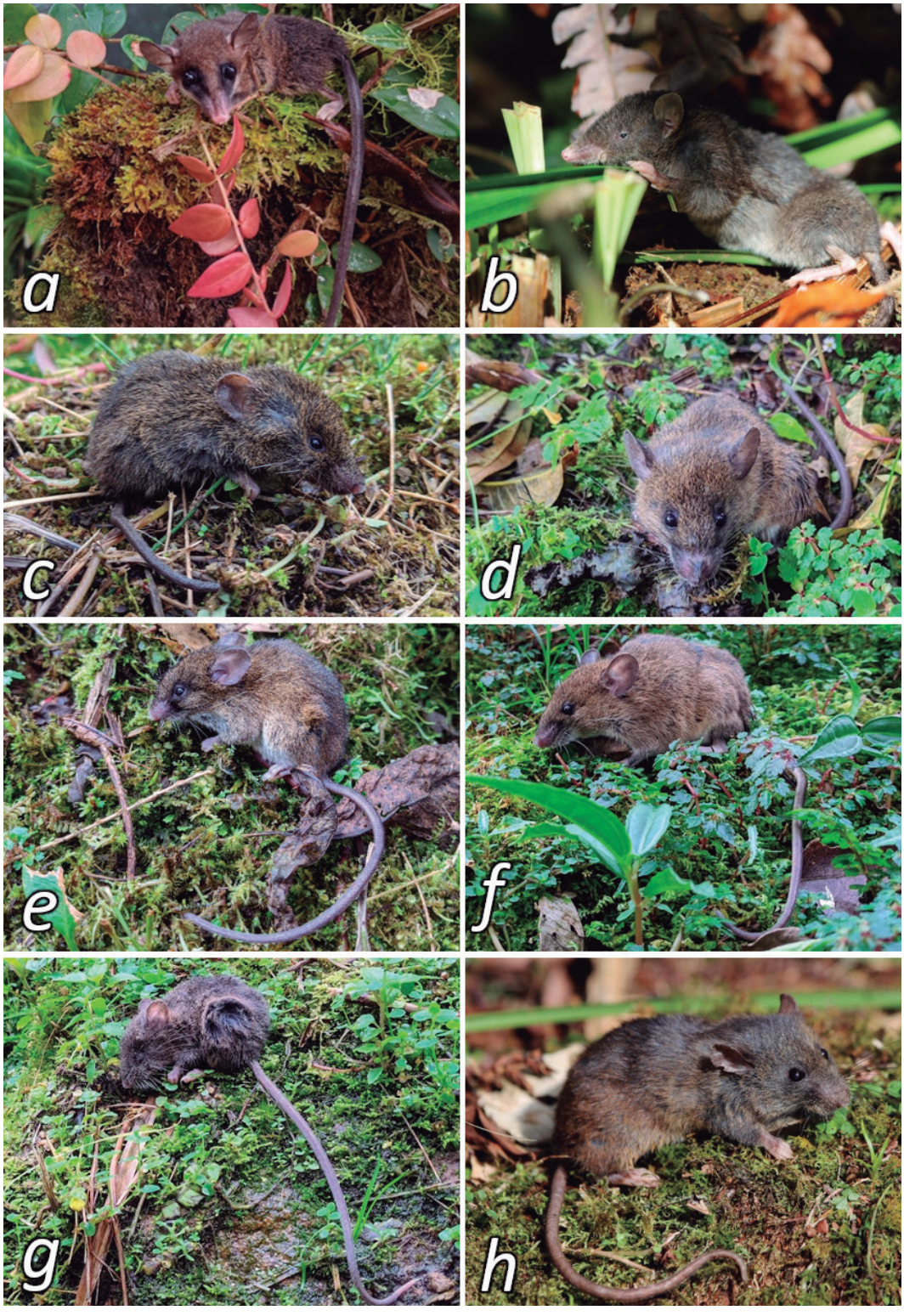
Recorded non-volant small mammal species: Didelphidae: a) *Marmosops caucae*; Caenolestidae: b) *Caenolestes condorensis*; Cricetidae: c) *Akodon aerosus*, d) *Nephelomys albigularis*, e) *Oreoryzomys balneator*, f) *Thomasomys aureus*, g) *Thomasomys caudivarius*, h) *Thomasomys taczanowskii*. Photos by: T. E. Lee Jr.

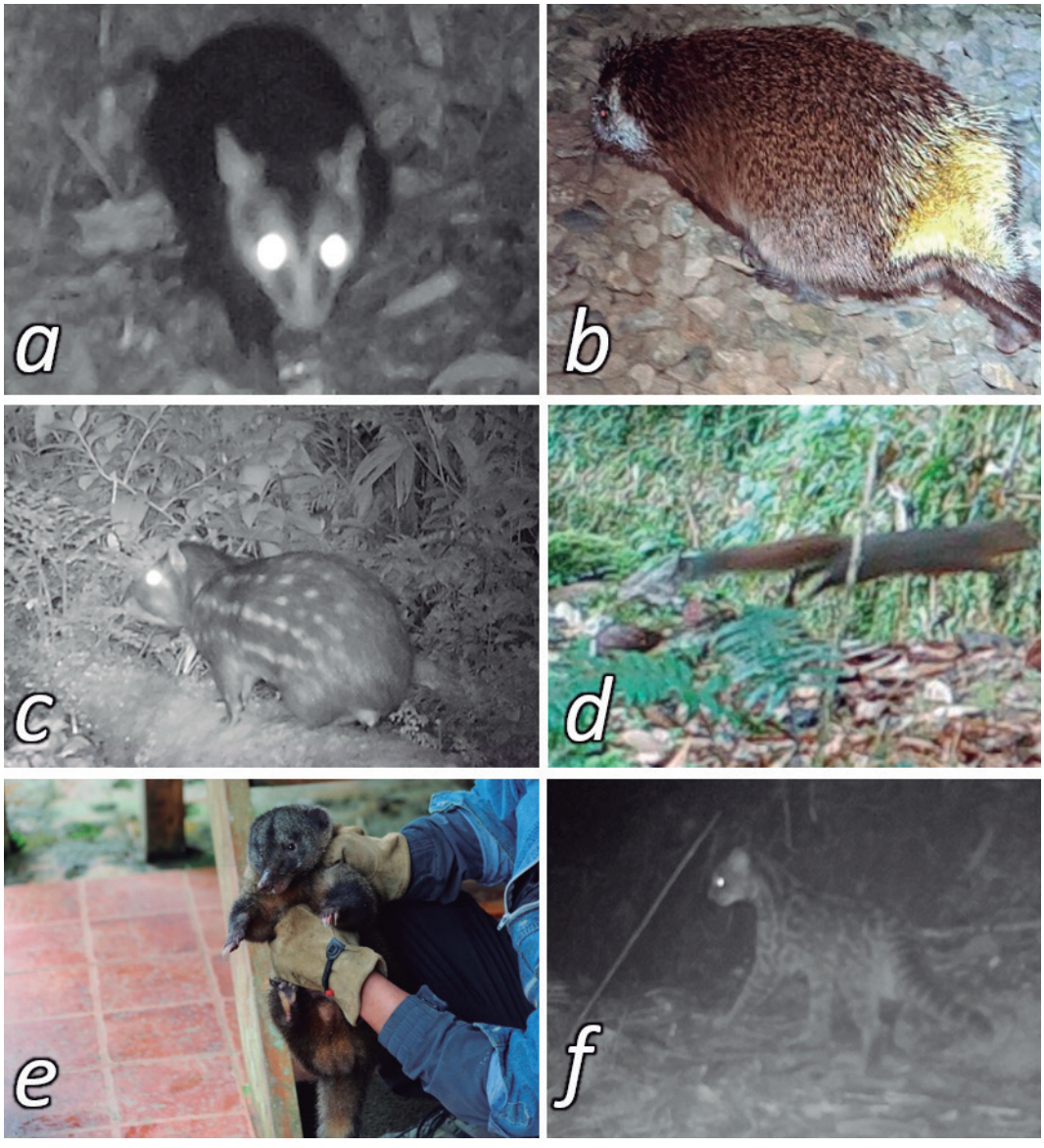
Appendix A

Mammal species recorded at Tapichalaca Reserve, Zamora Chinchipe, Ecuador



Appendix B

Mammal species recorded at Tapichalaca Reserve, Zamora Chinchipe, Ecuador



Recorded middle and large sized species. Didelphidae: a) *Didelphis pernigra*; Erethizontidae, b) *Coendou rufescens*; Cuniculidae: c) *Cuniculus taczanowskii*; Sciuridae: d) *Syntheosciurus granatensis*; Procyonidae: e) *Nasua olivacea*; Felidae: f) *Leopardus tigrinus*. Photos by: T. E. Lee Jr.

Appendix C
Mammal species recorded at Tapichalaca Reserve, Zamora Chinchipe, Ecuador

Recorded volant small mammal species. Phyllostomidae: a) *Anoura geoffroyi*, b) *Sturnira bidens*, c) *S. erythromos*; Vespertilionidae: d) *Myotis oxyotus*. Photos by: T. E. Lee Jr.