Discovery of the world’s highest-dwelling mammal

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Environmental limits of animal life are invariably revised when the animals themselves are investigated in their natural habitats. Here we report results of a scientific mountaineering expedition to survey the high-altitude rodent fauna of Volcán Llullaillaco in the Puna de Atacama of northern Chile, an effort motivated by video documentation of the high-altitude rodent fauna of Volcán Llullaillaco in the Puna de Atacama of northern Chile, an effort motivated by video documentation of mice (genus *Phyllotis*) at a record altitude of 6,205 m. Among numerous trapping records at altitudes of >5,000 m, we captured a specimen of the yellow-rumped leaf-eared mouse (*Phyllotis xanthopygus rupestris*) on the very summit of Llullaillaco at 6,739 m. This summit specimen represents an altitudinal world record for mammals, far surpassing all specimen-based records from the Himalayas and other mountain ranges. This discovery suggests that we may have generally underestimated the altitudinal range limits and physiological tolerances of small mammals simply because the world’s high summits remain relatively unexplored by biologists.

**Results and Discussion**

On a 2013 mountaineering expedition to Volcán Llullaillaco, M.F. and T.B. filmed a mouse (identified as *Phyllotis* spp.) scurrying across a snowfield at 6,205 m above sea level (24°43’05.2”S, 68°33’32.3”W) (Movie S1), an altitude that exceeds existing records for wild mammals. This sighting motivated a subsequent high-altitude trapping expedition in February 2020, led by J.F.S., M.Q.-C., and G.D. During this expedition, we live-trapped rodents from ecologically diverse sites on the altiplano and puna spanning >4,300 m of vertical relief (Fig. 1). On Volcán Llullaillaco, we live-trapped rodents in and around Aguadas de Zorritas (4,140 m to 4,360 m), base camp at Ruta Normal (4,620 m), base camp at Ruta Sur (5,070 m), high camp at Ruta Sur (5,850 m), and the volcano summit (6,739 m). In total, we collected museum voucher specimens of 80 mice representing four species: Andean altiplano mouse (*Abrothrix andina*), altiplano laucha (*Eligmodontia puerulus*), yellow-rumped leaf-eared mouse (*Phyllotis xanthopygus*), and Lima leaf-eared mouse (*Phyllotis limatus*). We collected *Eligmodontia puerulus* and *Abrothrix andina* at maximum altitudes of 4,099 and 4,620 m, respectively; these altitudes approximate or exceed previous records for these species (7,8). Our altitudinal records for *P. limatus* and *P. xanthopygus* (5,070 and 6,739 m, respectively) far exceed existing records for both species (9–11).

We captured the 6,739-m specimen of *P. xanthopygus* on the very summit of Llullaillaco (24°43’23.5”S, 68°32’20.8”W) (Movie S2). This summit specimen represents an altitudinal world record for mammals, far surpassing all specimen-based records from the Himalayas and elsewhere in the Andes. An extensive review of published accounts indicates that the large-eared pika, *Ochotona macrotis* (Lagomorpha), was the previous record holder. Although the highest specimen-based records for this species are from 5,182 m in the Himalayas (US National Museum 198648 and 198649), credible sightings at 6,130 m were reported from a 1921 Everest expedition (12).

Phylogenetic analysis of cytochrome b (*cytb*) sequences corroborated the species identifications of our record specimen of *P. limatus* and *P. xanthopygus* and revealed close relationships with conspecific specimens from elsewhere in northern Chile, northern Argentina, and southern Peru (Fig. 2). The summit specimen (GD 2097) groups with those of previously collected altiplano specimens of *P. xanthopygus rupestris* (13). Moreover, the *cytb* haplotype of this summit specimen is identical to that of another *P. x. rupestris* specimen (LCM1780) collected at Toconao, Chile, a 2,500-m locality ca. 180 km NNE of Volcán Llullaillaco. Similarly, two other specimens of *P. x. rupestris* collected at different altitudes (GD 2082 at 4,406 m and GD 2095 at 5,069 m) on Volcán Llullaillaco share identical *cytb* haplotypes with a specimen (LCM1737) collected at the mouth of the Loa River on the Pacific coast, ca. 400 km NW of Volcán Llullaillaco. Thus, not only does *P. x. rupestris* range from sea level to the crest of the Andean Cordillera at 6,739 m (the broadest altitudinal distribution of any...
mammal), but individuals found at opposite extremes of this vast range share identical cytB haplotypes. Our capture of *P. x. rupestris* on the summit of Llullaillaco suggests that we may have generally underestimated the altitudinal range limits and physiological tolerances of small mammals simply because the world’s high summits remain relatively unexplored by biologists. The upper range limits of many vertebrate taxa are not precisely demarcated, and putative altitudinal records for many taxa exist as unverified sightings or reports in mountaineering expedition accounts rather than as voucher specimens in museum collections. Our discoveries prompt many evolutionary and ecological questions. Given the exceptionally broad altitudinal range of *P. xanthopygus*, have mice from the high Andes evolved genetically based adaptations to hypoxia that distinguish them from lowland conspecifics? To what extent is the ability to tolerate such a broad range of environmental conditions attributable to acclimatization (physiological plasticity)? Given that mice inhabiting the upper reaches of Llullaillaco are living >2,000 m above the upper limits of green plants, what are they eating? Such questions can be answered by future mountaineering expeditions in the Humboldtian tradition that combine high-altitude exploration and scientific discovery.

**Materials and Methods**

**Specimen Collection.** We captured mice using Sherman live traps, except for the specimen from the Llullaillaco summit, which was captured by hand (Movie S2). We killed mice in the field and prepared them as museum specimens, all of which are housed at the Colección de Mamíferos of the Universidad Austral de Chile, Valdivia, Chile. Tissue samples from Argentinian and Peruvian specimens were obtained as loans from the collections of Centro Nacional Patagónico, Puerto Madryn, Argentina, and Louisiana State University Museum of Natural Science, Baton Rouge, LA.

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Fig. 1. High-altitude survey. Map showing collecting localities in the altiplano and Puna de Atacama (A), including Volcán Llullaillaco (B), Región de Antofagasta, Chile. (C) View of Volcán Llullaillaco (6,739 m [24°43.235′S, 68°32.208′W]) from the west.
All mice were collected in accordance with permissions to J.F.S. from the following Chilean government agencies: Servicio Agrícola y Ganadero (Resolución extenta #209/2020), Corporación Nacional Forestal (Autorización nos. 171219 and 1501221), and Dirección Nacional de Fronteras y Límites del Estado (Autorización de Expedición Científica #68). All mice were live-trapped and handled in accordance with protocols approved by the Institutional Animal Care and Use Committee at the University of Nebraska (Project ID 1919). Argentinian samples were exported under Permit #3938/03 (Resolución extenta #209/2020), Corporación Nacional Forestal (Autorización #3938/03). We thank Ulyses Pardiñas, Mark Hafner, and Donna Dittmann for tissue loans, and Cristina Dorador for logistical support. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson (Grant NGS-68495R-20), a grant to G.D. from the Fondo Nacional de Desarrollo de la Salud #2014-022, a grant to M.Q.-C. from the NSF (Grant DEB-0108422). We thank Ulyses Pardiñas, Mark Hafner, and Donna Dittmann for tissue loans, and Cristina Dorador for logistical support. This work was funded by grants to J.F.S. from the NIH (Grant HL087216), NSF (Grant OIA-1762494), and National Geographic Society (Grant NGS-68495R-20), a grant to G.D. from the Fondo Nacional de Desarrollo Científico y Tecnológico (Grant Fondecyt 1180366), and a grant to S.J.S. from the NSF (Grant DEB-0108422). We thank Ulyses Pardiñas, Mark Hafner, and Donna Dittmann for tissue loans, and Cristina Dorador for logistical support. J.F.S. and M.Q.-C. thank Mario Pérez-Mamani and Juan Carlos Briceño for assistance and companionship in the field.

**Data Availability.** All DNA sequences are available in GenBank (MT183676 to MT183689).

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