

# *Sciurus stramineus* (Rodentia: Sciuridae)

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**Abstract:** *Sciurus stramineus* Eydoux and Souleyet, 1841, is a large-bodied squirrel commonly called the Guayaquil squirrel. *S. stramineus* is characterized by a distinct grizzled-gray pelage with dark feet and ears, a long tail, and a distinctive white “collar” behind the ears. It is native to the western slope of the Andes, occurring from dry or humid tropical forests at sea level to high-elevation montane forests up to 2,000 m in Ecuador and Peru. *S. stramineus* is adaptable, adjusting to anthropogenic changes and living close to human settlements, in coffee plantations, with an introduced population in Lima, Peru. Because of a tolerance for living in proximity to humans, *S. stramineus* is also a concern for transmission of diseases such as leptospirosis and Chagas disease.

**Key words:** Ecuador, introduced species, Peru, sciurid, tree squirrel

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## *Sciurus stramineus* Eydoux and Souleyet, 1841 Guayaquil Squirrel

*Sciurus stramineus* Eydoux and Souleyet, 1841:329. Type locality “Peru, Piura Dept., Omatope.”

*Sciurus nebouxii* I. Geoffroy Saint-Hilaire, 1855:163. Type locality “Near Payta, Peru.”

*Macroxus fraseri* Gray, 1867:430. Type locality “Republic of Ecuador.”

*Sciurus hypopyrrhus* Allen, 1877:746. Part, not *Sciurus hypopyrrhus* Wagler, 1831 (see “Nomenclatural Notes”).

*Sciurus tephrogaster* Allen, 1877:763. Part, *Macroxus fraseri* Gray, 1867 (see “Nomenclatural Notes”).

*Sciurus variabilis* Allen, 1877:768. Part, not *Sciurus variabilis* I. Geoffroy Saint-Hilaire, 1832 (see “Nomenclatural Notes”).

*Sciurus stramineus typicus* Thomas, 1900:151. Usage equivalent to *Sciurus stramineus stramineus* and not intended as a new name.

*Sciurus stramineus Nebouxii*: Thomas, 1900:151. Name combination.

*Sciurus stramineus guayanus* Thomas, 1900:150. Type locality “Balzar Mountains, upper Palenque River, western Ecuador. Another specimen from Chongan.”

*Simosciurus stramineus stramineus*: Allen, 1915:281. Name combination.

*Simosciurus stramineus nebouxii*: Allen, 1915:282. Name combination.

*Simosciurus stramineus guayanus*: Allen, 1915:283. Name combination.

*Simosciurus stramineus zarumae* Allen, 1915:284. Type locality “Zaruma, southwestern Ecuador.”

**CONTEXT AND CONTENT.** Order Rodentia, superfamily Sciuroidea, family Sciuridae, subfamily Sciurinae, tribe



**Fig. 1.**—Adult *Sciurus stramineus* of introduced population in Lima, Peru; photograph by MJM taken in Parque de las Leyendas.

*Sciurini*, subgenus *Guerlinguetus* (Cabrera 1961; Thorington and Hoffmann 2005). *S. stramineus* is monotypic (Thorington and Hoffmann 2005).

**NOMENCLATURAL NOTES.** Historically, the assignment of South American squirrel specimens to genus and species was wrought with difficulty due to the extremely variable pelage color patterns of this group, vague records for type localities and unfamiliarity with the terrain, and the small number of samples available for examination (Allen 1915; Alston 1878). Such paucity of information caused a great deal of confusion regarding name assignments for *Sciurus stramineus*, along with many other South American squirrel species.

In his 1867 *Synopsis of the species of American squirrels in the collection of the British Museum*, J. E. Gray described 18 new Neotropical tree squirrel species, and assigned *S. stramineus* to *Macroxus fraseri*. Gray's synopsis frustrated later taxonomists trying to unravel his name assignments, which were associated with inadequate descriptions necessary for proper classifications (Allen 1877, 1915; Alston 1878; Gray 1867). As a result of this confusion, J. A. Allen (1877) divided likely specimens of *S. stramineus* into 3 different species: *Sciurus tephrogaster* (where he placed *M. fraseri* of Gray), *Sciurus variabilis* (where he placed *S. stramineus* of Eydoux and Souleyet), and inadvertently *Sciurus hypopyrrhus*, under which he included 3 specimens from Guayaquil, Ecuador, which Allen later states as belonging to *S. stramineus* (Allen 1877; Allen 1915:153).

In 1878, with access to more South American specimens, E. R. Alston again reviewed the Neotropical tree squirrels and raised *S. stramineus* to a unique species, as “This curious squirrel which appears to be the sole representative of the genus in western Peru . . .” (Alston 1878:665). In 1900, O. Thomas recognized 3 distinct subspecies of *S. stramineus* based on different pelage color patterns and geographic locations (Thomas 1900). Upon a 2nd review of South American Sciuridae, Allen decided to “eliminate the genus *Sciurus* from the American biota and instead use generic divisions as seen properly to express the diversity of the sciurid types of North and South America” (Allen 1915:171), and so assigns *S. stramineus* to the new genus *Simosciurus* with 4 distinct subspecies based on pelage color patterns and geographic location. The 4 subspecies recognized by Allen (1915) and Ellerman (1940) were subsumed into a single monotypic group, because of significant morphological and geographical overlap among all forms (Cabrera 1961).

The specific epithet *stramineus* means made of straw, or straw colored (Latin-Dictionary 2008). Common names include Guayaquil squirrel (Wilson and Cole 2000), South American gray squirrel (Smithsonian Institution Board of Regents 1948), Fraser's squirrel (Sclater 1878), and in French, ecureuil paillé (Eydoux and Souleyet 1841). Local names for *S. stramineus* from Peru and Ecuador include ardilla sabanera, ardilla parda, ardilla nuca (nucha) blanca,

ardilla mora, ardilla negra; with sabanera referring to savanna, parda and mora referring to color, and nuca referring to the back of the neck (Emmons and Feer 1999; Pacheco et al. 2009; Tirira 1999).

## DIAGNOSIS

The range of *Sciurus stramineus* only overlaps with that of the red-tailed squirrel (*Sciurus granatensis*) north of Guayaquil, Ecuador. *S. granatensis* is generally smaller (length of head and body range 200–285 mm compared to 180–320 mm with a mean of 252.8 mm in *S. stramineus* [Hayssen 2008]), with smaller ears (length of ear range 16–36 mm compared to 28–39 mm in *S. stramineus*), and more brown overall with a red-tinged or bright ochraceous tail (Emmons and Feer 1999; Nitikman 1985) compared to *S. stramineus*. Jaw shape and lever arm lengths of *S. stramineus* are indistinguishable from those of North American *Sciurus*, the only South American species for which this is true (Swiderski and Zelditch 2010).

## GENERAL CHARACTERS

*Sciurus stramineus* is a large-bodied tree squirrel with a long, slender, gray tail, long, dark ears, and 4 pairs of mammae (Allen 1915; Emmons and Feer 1999). Color is variable with 2 morphs: a darker morph from the Ecuador lowlands: shoulders grizzled black and white; rump and base of tail grizzled dull orange and black with head and ears black; feet black or white; and underparts brown or reddish (Emmons and Feer 1999); and a lighter and grayer morph from southern Ecuador and northern Peruvian highlands: upper body and tail heavily frosted with white such that body and tail appear light gray; rump washed with faint orange or buff; neck behind ears is pure white or pale yellow with black ears; and underparts gray (Fig. 1; Emmons and Feer 1999). Variations in color pattern include: ventral surface and feet heavily washed with yellowish tawny to rufous (Allen 1915); collar on the back of neck can range from absent (Allen 1915) to buff to white; the reddish to orange color on the rump can be absent; and black morphs with black venter and dorsum with contrasting white dorsal collar and a few dorsal spots (Eisenberg and Redford 1999). Variable white spots, mainly on the dorsum, consisting of irregular white tufts of hair longer than the surrounding pelage, are not thought to be diagnostic but the result of past injuries or insect bites (Alston 1878; Eisenberg and Redford 1999; Gray 1867).

External measurements (ranges or means; mm) for *S. stramineus* were: total length: 530–590 (Eisenberg and Redford 1999); length of tail: 250–330 (Eisenberg and Redford 1999; Emmons and Feer 1999), length of tail for females: 292.1, length of tail for males: 275.4, adult length of

tail (sex unknown): 310 (Hayssen 2008); length of hind foot: 50–65 (Eisenberg and Redford 1999; Emmons and Feer 1999); length of ear: 28–39 (Eisenberg and Redford 1999; Emmons and Feer 1999); length of head and body: 180–320 (Emmons and Feer 1999), length of head and body for females: 250.3, length of head and body for males: 251.3, adult length of head and body (sex unknown): 256.7 (Hayssen 2008); and body mass from 1 individual: 470 g (Eisenberg and Redford 1999). Cranial measurements (range; mm) were: total length: 58.2–60.0; zygomatic breadth: 32–33; interorbital breadth: 18–20; postorbital breadth: 17–18; breadth of braincase: 22.0–23.5; diastema: 13.2–14.5; and length of maxillary toothrow: 10.0–10.5 (Allen 1915). The percentage of toothrow comprising the total length of skull for the *stramineus* group was 17.6 (range: 17.2–18.0—Ellerman 1940).

## DISTRIBUTION

*Sciurus stramineus* ranges from southwestern Ecuador to northwestern Peru on the western slope of the Andes between sea level and 300–2,000 m in elevation (Fig. 2). *S. stramineus* inhabits dry, humid, and montane forests including secondary and mature forests, and has been observed in coffee plantations. In the southern portion of its range it occupies more high-elevation forests between 1,400 and 2,000 m in elevation, whereas in the northern portion of its range it occurs in the highlands and in both humid and dry forests at sea level (Eisenberg and Redford 1999; Emmons and Feer 1999). An introduced population also occurs in parks, tree-lined streets, and zoos in Lima, Peru (Jessen et al. 2010; Montes 2009).

## FOSSIL RECORD

The Miocene represents a period of increased radiation of squirrel species, including *Sciurus*, which experienced extremely rapid expansion into South America approximately 3.1 million years ago (Black 1972; Mercer and Roth 2003), with a net rate of diversification calculated as 0.92 lineages per million years (Roth and Mercer 2008). Skeletal material of a *Sciurus* was recorded from Challuabamba, about 10 km from Cuenca, Ecuador, with the origin dated as 2200 BC to 1200 BC (Stahl 2005). At present, *Sciurus stramineus* is the only squirrel found in the vicinity of Cuenca.

## FORM AND FUNCTION

The skull of *Sciurus stramineus* has a very short rostrum, very broad and short nasals (22% of total length of the skull; 60% of the interorbital breadth), with a broad and heavy malar, and zygomata slightly anteriorly convergent (Fig. 3;

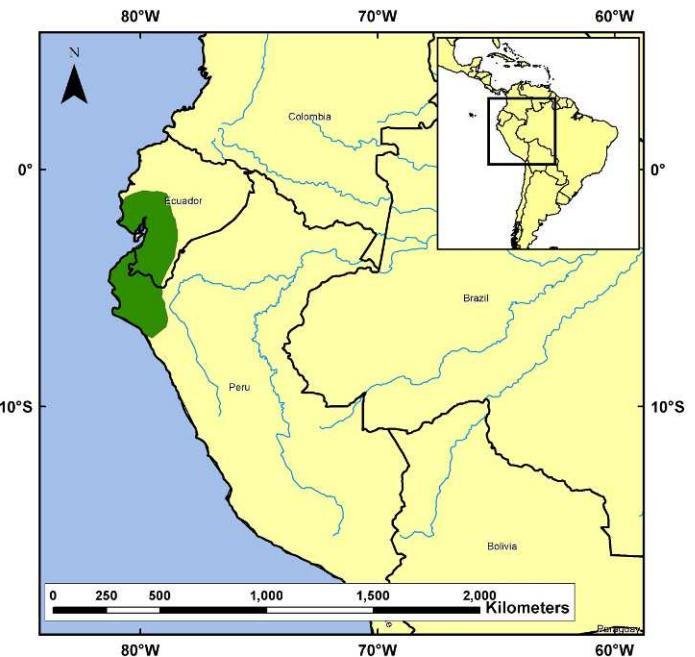


Fig. 2.—Geographic distribution of *Sciurus stramineus* in South America.

Allen 1915). *S. stramineus* has a large area on the frontal bone, dorsolateral to the postorbital process, for origin and passage of the temporalis muscle and the posterior angle of the jaw extends laterally beyond the zygomatic arch (Roth 1996). The frontal bone has a distinctly pointed postorbital process (Roth 1996). The mechanical advantages of the superficial masseter, anterior deep masseter, and temporalis muscles as well as scaled jaw area are intermediate among the *Sciurus* (Velhagen and Roth 1999). Dental formula is i 1/1, c 0/0, m 4/4, total 20; however, some specimens are known to have an upper premolar, p 1/0, giving a total of 22 (Allen 1915; Jentink 1883).

## ECOLOGY

*Sciurus stramineus* is observed in both mature and secondary forests (Emmons and Feer 1999). On the central coast of Ecuador within the semideciduous lowland forest (Portoviejo County, Manabí Province at 248 m and Maonta Abajo at 290 m), *S. stramineus* inhabits forest types characterized by “thorny vegetation, a disperse tree stratum, and dense understory with plants that lose their leaves once a year” (Suarez-Davalos et al. 2010:82). These areas are close to human settlements and the landscape is fragmented with a mix of forest and agricultural areas for cultivation of corn and papaya.

*Sciurus stramineus* inhabits Cerros de Amotape National Park near the coast of northern Peru. Elevation ranges from 200 to 1,613 m, and the general vegetation type is characterized as Ecuadorian Dry Forest, composed of



**Fig. 3.**—Dorsal, ventral, and lateral views of skull and lateral view of mandible of *Sciurus stramineus* (Field Museum of Natural History 80996), from Chiclayo, Lambayeque Department, Cabache, 460 m; Perú. Greatest length of skull is 60 mm; no information on sex. Photos by B. Patterson used with permission.

mountain thorny, very dry forest, and tropical and dry forest with representative species including *Prosopis juliflora* (bayahonda blanca), *Bombax* (silkcotton trees), *Tillandsia* (bromeliads), *Loxopterygium huasango*, *Capparis angulata* (sapote), and *Caesalpinia corymbosa*. Additional mammals within the park include white-tailed deer (*Odocoileus virginianus*), collared peccary (*Pecari tajacu*), puma (*Felis concolor*), tayra (*Eira barbara*), and probably ocelot (*Leopardus pardalis*) and jaguar (*Panthera onca*—International Union for Conservation of Nature and Natural Resources 1982).

In the dry plains and forests found along the northeastern coast of Peru, observed seedeaters include *P. gerbillus* (published as *Phyllotis*, gerbil leaf-eared mouse), *S. stramineus*, *Oligoryzomys arenalis* (sandy pygmy rice rat), and white-tailed deer. Other important species in this ecosystem include *Dicrodon guttulatum* (Peru desert tegu), *Microlophus occipitalis* (knobbed Pacific iguana), *Tropidurus peruvianus* (Atacamen Pacific iguana), *Callopistes flavipunctatus* (false monitor lizard), *Iguana iguana* (green iguana), *Athene cunicularia* (burrowing owl), migrant *Falco peregrinus* (peregrine falcon), *Falco sparverius* (American kestrel), *Buteo polyosoma* (variable hawk), and *Circus cinereus* (cinereus harrier). The most common predator in this system is *Lycalopex sechurae* (Sechuran fox), a known predator of *S. stramineus* (Cossíos 2010; Erdmann et al. 2008). Dominant trees of this area include sapote, *Acacia macracantha* (long-spine acacia or espino), and *Prosopis pallida*, a species of mesquite (kiawe, algarroba, or bayahonda—Erdmann et al. 2008).

The introduced population of *S. stramineus* in Lima, Peru, feeds on dried fruits, seeds, insects, flowers, mushrooms, plant stalks, and sap (Montes 2009). In dry coastal forests of northeastern Peru, *S. stramineus* is noted as being among a main group of seed-eating rodents (Erdmann et al. 2008).

*Sciurus stramineus* is a vector for leptospirosis. Of 35 individuals (15 adults and 20 juveniles) sampled from the introduced population at Parque de las Leyendas Zoo in Lima, Peru, 82.3% (86.7% of adults and 80% of juveniles) possessed antibodies against *Leptospira* (Montes 2009), indicating *S. stramineus* could pose a risk of spreading disease to other mammals, including humans. Sylvatic plague (*Yersinia pestis*) also is known in *S. stramineus* in Peru (Garnham 1949), where it appears to be a primary reservoir for the disease (Pollitzer 1952). Nests of *S. stramineus* are associated with triatomines, hemipteran insect vectors that carry the protozoan parasite, *Trypanosoma cruzi*, responsible for Chagas disease. Of 81 nests of *S. stramineus* searched near human settlements in Loja Province, Ecuador, 11 (13.6%) were infested with the triatomine *Rhodnius ecuadoriensis*. Nests of *S. stramineus* contained a total of 103 individuals of *R. ecuadoriensis*, although mouse and bird nests in the same sylvatic habitat were not infested (Grijalva and Villacis 2009). Nests of *S.*



**Fig. 4.**—Adult *Sciurus stramineus* of introduced population in Lima, Peru; photograph taken in Parque de las Leyendas. Photograph by D. Montes used with permission.

*stramineus* > 5 m above the ground, located close to human domiciles, and in trees other than palms were highly correlated with triatomine density (Suarez-Davalos et al. 2010). The flea *Polygenis litargus* has been recorded on *S. stramineus* from Peru (Jordan 1950; Macchiavello 1957). An *Amblyomma* tick, likely related to *A. maculatum*, is known to parasitize *S. stramineus* in Peru (Need et al. 1991).

## HUSBANDRY

*Sciurus stramineus* was bred in captivity at the Parque de las Leyendas in Lima, Peru, at least as long ago as 1967 (Zoological Society of London 1969). *S. stramineus* persists in cities, landscapes fragmented by anthropogenic activity, and in captivity, consuming a wide variety of food items, including food prepared for captive zoo animals (e.g., seeds, fruits, and vegetables) and ornamental flowers at Parque de las Leyendas in Lima, Peru (Fig. 4; Montes 2009; this observation was made by MJM as well). One individual has lived in captivity for 7.3 years (Weigl 2005).

## BEHAVIOR

*Sciurus stramineus* is diurnal and arboreal and has been observed in both mature and secondary forests (Emmons and Feer 1999). In cities such as Guayaquil, Ecuador, and Lima, Peru, *S. stramineus* is commonly observed in parks and tree-lined streets, moving on the ground, in trees, and on power lines (Jessen et al. 2010; Montes 2009). Nests are loosely constructed of woven sticks, 30 cm diameter, and located in trees other than palms, above 5 m, and can be in close proximity to houses (Suarez-Davalos et al. 2010).



**Fig. 5.**—Adult male *Sciurus stramineus* of introduced population in Lima, Peru; photograph taken in Parque de las Leyendas. Photograph by D. Montes used with permission.

## GENETICS

Protein variation based on electrophoresis of 27 isolates from 7 species and 4 genera (*Sciurus*, *Microsciurus*, *Sciurillus*, and *Tamiasciurus*) indicates that the genus *Sciurus* is paraphyletic, with *S. stramineus* falling within the same clade as North American *Sciurus* and *Microsciurus* (Hafner et al. 1994). More recent studies based on the mitochondrial cytochrome-*b* gene (Oshida and Masuda 2000; Steppan et al. 2004) and recombination activating gene 1 (RAG1—Steppan et al. 2004) corroborate the placement of *S. stramineus* within a clade with other New World *Sciurus*, suggesting rapid radiation of *Sciurus* in the New World (Oshida and Masuda 2000; Roth and Mercer 2008) and also close affinity to *Microsciurus* (Steppan et al. 2004).

## CONSERVATION

*Sciurus stramineus* is ranked by the International Union for Conservation of Nature and Natural Resources as “Least Concern” and the current population trend for *S. stramineus* is unknown (Duckworth and Koprowski 2008). However, *S. stramineus* is described as locally common and hunted for food (Duckworth and Koprowski 2008; Emmons and Feer 1999). *S. stramineus* serves as an excellent indicator of biodiversity in the equatorial Pacific of South America (Peralvo et al. 2007). Threats may include deforestation and

habitat fragmentation from timber and agricultural practices because habitat of *S. stramineus* has declined by 62.3% over historical availability (Koprowski and Nandini 2008; Peralvo et al. 2007). *S. stramineus* occurs within 3 protected areas in Peru: Zona Reservada de Tumbes, Parque Nacional Cerros de Amotape, and Coto de Caza “El Angolo” (El Angola Game Preserve), which together comprise the Noroeste Biosphere Reserve (Leal-Pinedo and Linares-Palomino 2005).

*Sciurus stramineus* is frequently captured and available worldwide in the pet trade, with captive individuals reported from locations as distant as Japan (Jessen et al. 2010; Oshida and Masuda 2000; Pacheco 2002). *S. stramineus* adapts to a wide array of forest types from very xeric coastal forests to humid, tropical, high-elevation forests (Eisenberg and Redford 1999; Emmons and Feer 1999). *S. stramineus* persists within and in close proximity to human population centers (Fig. 5; Grijalva and Villacis 2009; Jessen et al. 2010; Montes 2009; Suarez-Davalos et al. 2010). The capacity of *S. stramineus* to thrive in many different ecological conditions is a major reason why in Peru *S. stramineus* is invasive where it has been translocated, such as Parque de las Leyendas Zoo in Lima (Montes 2009).

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## LITERATURE CITED

- ALLEN, J. A. 1877. Sciuridae. Monographs of North American Rodentiae. Department of the Interior Report of the United States Geological Survey of the Territories 11:746–768.
- ALLEN, J. A. 1915. Review of the South American Sciuridae. Bulletin of the American Museum of Natural History 34:137–309.
- ALSTON, E. R. 1878. On the squirrels of the Neotropical region. Proceedings of the Zoological Society of London 46:656–670.
- BLACK, C. C. 1972. Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). Pp. 305–322 in Evolutionary biology (T. Dobzhansky, M. Hecht, and W. Steere, eds.). Vol. 6. Plenum Press, New York.
- CABRERA, A. 1961. Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales, Ciencias Zoológicas 4:373–374.
- COSSIOS, E. D. 2010. *Lycalopex sechurae* (Carnivora: Canidae). Mammalian Species 42:1–6.
- DUCKWORTH, J. W., AND J. L. KOPROWSKI. 2008. *Sciurus stramineus*. International Union for Conservation of Nature and Natural Resources Red list of threatened species. www.iucnredlist.org, accessed 22 February 2011.
- EISENBERG, J. F., AND K. H. REDFORD. 1999. Mammals of the Neotropics. Vol. 3. The central Neotropics: Ecuador, Peru, Bolivia, Brazil. University of Chicago Press, Chicago, Illinois.
- ELLERMAN, J. R. 1940. The families and genera of living rodents. Vol. I. Rodents other than Muridae. With a list of named forms (1758–1936) by R. W. Hayman and G. W. C. Holt. British Museum (Natural History), London, United Kingdom.
- EMMONS, L. H., AND F. FEER. 1999. Neotropical rainforest mammals. 2nd ed. University of Chicago Press, Chicago, Illinois.
- ERDMANN, W., N. SCHULZ, M. RICHTER, AND E. F. RODRIGUEZ. 2008. Efectos del fenómeno del Niño 1997–1998 en la vegetación del desierto de Sechura, Región Piura hasta el año 2008. Arnaldoa 15:63–86.
- EYDOUX, F., AND L. F. A. SOULEYET. 1841. Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette la Bonite, commandée par M. Vaillant. Zoologie, Par MM. Eydoux et Souleyet, médecins de l’expédition. Tome I. Partie II. Arthus Bertrand, Éditeur, Paris, France.
- GARNHAM, P. C. C. 1949. Distribution of wild-rodent plague. Bulletin of the World Health Organization 2:271–278.
- GEOFFROY SAINT-HILAIRE, I. 1832. Essai sur le genre *Sciurus*, et description de six nouvelle espèces. Pp. 154–176. Magasin de Zoologie, Series 2, Classe I, Plate 4.
- GEOFFROY SAINT-HILAIRE, I. 1855. Mammifères, Par M. Isidore Geoffroy Saint-Hilaire. Voyage autour du monde sur la frégate la *Vénus*, commandée par Abel de Petit-Thouars. Zoologie: mammifères, oiseaux, peuples, et poissons. Gide et J. Baudry, Éditeurs Paris, France.
- GRAY, J. E. 1867. Synopsis of the species of American squirrels in the collection of the British Museum. Annals and Magazine of Natural History, Including Zoology, Botany, and Geology Series 20, 3: 415–434.
- GRITALVA, M. J., AND A. G. VILLACIS. 2009. Presence of *Rhodnius ecuadoriensis* in sylvatic habitats in the southern highlands (Loja Province) of Ecuador. Journal of Medical Entomology 46:708–711.
- HAFNER, M. S., L. J. BARKLEY, AND J. M. CHUPASKO. 1994. Evolutionary genetics of the New World tree squirrels (tribe Sciurini). Journal of Mammalogy 75:102–109.
- HAYSEN, V. 2008. Patterns of body and tail length and body mass in Sciuridae. Journal of Mammalogy 89:852–873.
- INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES. 1982. International Union for the Conservation of Nature directory of Neotropical protected areas. IUCN Commission on National Parks and Protected Areas (CNPPA). Tycooly International Publishing Limited, Dublin, Ireland.
- JENTINK, F. A. 1883. List of the specimens of squirrels in the Leyden Museum. Notes from the Leyden Museum 5(13):91–144.
- JESSEN, R. R., M. J. MERRICK, J. L. KOPROWSKI, AND O. RAMIREZ. 2010. Presence of Guayaquil squirrels on the central coast of Peru: an apparent introduction. Mammalia 74:443–444.
- JORDAN, K. 1950. Notes on a collection fleas from Peru. Bulletin of the World Health Organization 2:597–609.
- KOPROWSKI, J. L., AND R. NANDINI. 2008. Global hotspots and knowledge gaps for tree and flying squirrels. Current Science 95:851–856.
- LATIN-DICTIONARY.ORG. 2008. www.latin-dictionary.org, Accessed 28 February 2012.
- LEAL-PINEDO, J. M., AND R. LINARES-PALOMINO. 2005. The dry forests of the Biosphere Reserve of northwestern Peru: tree diversity and conservation status. Caldasia 27:195–211.
- MACCHIAVELLO, A. 1957. Estudios sobre peste selvática en América del Sur: II. Peste selvática en la región fronteriza de Perú y Ecuador. 2. El foco de peste selvática del distrito de Lancones, departamento de Piura, Perú. Boletín de la Oficina Sanitaria Panamericana 43:225–250.
- MERCER, J. M., AND V. L. ROTH. 2003. The effects of Cenozoic global change on squirrel phylogeny. Science 299:1568–1572.
- MONTES, D. 2009. Frecuencia de infección por *Leptospira* sp. en ardillas nuca blanca (*Sciurus stramineus*) silvestres en el Patronato del Parque de las Leyendas “Felipe Benavides Barreda.” Tesis por el título de Médico Veterinario, Universidad Nacional Mayor de San Marcos, Lima, Perú.
- NEED, J. T., W. E. DALE, J. E. KEIRANS, AND G. A. DASCH. 1991. Annotated list of ticks (Acari: Ixodidae, Argasidae) reported in Peru: distribution, hosts, and bibliography. Journal of Medical Entomology 28:590–597.
- NITIKMAN, L. Z. 1985. *Sciurus granatensis*. Mammalian Species 246: 1–8.

- OSHIDA, T., AND R. MASUDA. 2000. Phylogeny and zoogeography of six squirrel species from the genus *Sciurus* (Mammalia, Rodentia), inferred from cytochrome *b* gene sequences. *Zoological Science* 17:405–409.
- PACHECO, V. 2002. Mamíferos del Perú. Pp. 503–549 in *Diversidad y conservación de los mamíferos Neotropicales* (G. Ceballos and J. A. Simonetti, eds.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y Universidad Nacional Autónoma de México, México, Distrito Federal, México.
- PACHECO, V., R. CADENILLAS, E. SALAS, C. TELLO, AND H. ZEBALLOS. 2009. Diversidad y endemismo de los mamíferos del Perú. *Revista Peruana de Biología* 16:5–32.
- PERALVO, M., R. SIERRA, K. R. YOUNG, AND C. ULLOA-ULLOA. 2007. Identification of biodiversity conservation priorities using predictive modeling: an application for the equatorial Pacific region of South America. *Biodiversity and Conservation* 16:2649–2675.
- POLLITZER, R. 1952. Plague studies 6. Hosts of infection. *Bulletin of the World Health Organization* 6:381–465.
- ROTH, V. L. 1996. Cranial integration in the Sciuridae. *American Zoologist* 36:14–23.
- ROTH, V. L., AND J. M. MERCER. 2008. Differing rates of macroevolutionary diversification in arboreal squirrels. *Current Science* 95:857–861.
- SCLATER, P. L. 1878. Secretary's report on the additions to the Society's menagerie in April 1878. *Proceedings of the Scientific Meetings of the Zoological Society of London, for 1878*, part III containing papers read in May and June. The secretary on additions to the Menagerie. Part III May and June. Zoological Society of London, London, England.
- SMITHSONIAN INSTITUTION BOARD OF REGENTS. 1948. Appendix 7: report on the National Zoological Park. Pp. 101 in *Annual Report of the Board of Regents of The Smithsonian Institution Showing the Operations, Expenditures, and Condition of the Institution for the Year Ended June 30 1948*. Smithsonian Institution, Washington, D.C.
- STAHL, P. W. 2005. Selective faunal provisioning in the southern highlands of formative Ecuador. *Latin American Antiquity* 16:313–328.
- STEPPAN, S. J., B. L. STORZ, AND R. S. HOFFMANN. 2004. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. *Molecular Phylogenetics and Evolution* 30:703–719.
- SUAREZ-DAVALOS, V., O. DANGLES, A. G. VILLACIS, AND M. J. GRIJALVA. 2010. Microdistribution of sylvatic triatomine populations in central-coastal Ecuador. *Journal of Medical Entomology* 47:80–88.
- SWIDERSKI, D. L., AND M. L. ZELDITCH. 2010. Morphological diversity despite isometric scaling of lever arms. *Evolutionary Biology* 37:1–18.
- THOMAS, O. 1900. New South American mammals. *Annals and Magazine of Natural History*, Series 7, 5:150–151.
- THORINGTON, R. W., JR., AND R. S. HOFFMANN. 2005. Family Sciuridae. Pp. 754–818 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- TIRIRA, D. 1999. Mamíferos del Ecuador. Museo de Zoología, Centro de Biodiversidad y Ambiente, Pontificia Universidad Católica de Ecuador, Publicación Especial 2:1–392.
- VELHAGEN, W. A., AND V. L. ROTH. 1999. Scaling of the mandible in squirrels. *Journal of Morphology* 232:107–132.
- WAGLER, J. G. 1831. Mittheilungen über die Gattungen der Sippe *Bradypterus*. *Isis von Oken* 24:604–612.
- WEIGL, R. 2005. Longevity of mammals in captivity; from the living collections of the world: a list of mammalian longevity in captivity. Kleine Senckenberg-Reihe, Stuttgart, Germany.
- WILSON, D. E., AND F. R. COLE. 2000. Common names of the mammals of the world. Smithsonian Institution Press, Washington, D.C.
- ZOOLOGICAL SOCIETY OF LONDON. 1969. Species of wild animals bred in captivity during 1967, mammals. *International Zoo Yearbook* 9:215–244.

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