

## **Leopardus braccatus (Carnivora: Felidae)**

Authors: Barstow, Anita L, and Leslie, David M

Source: Mammalian Species, 44(1) : 16-25

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1644/891.1>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## *Leopardus braccatus* (Carnivora: Felidae)

ANITA L. BARSTOW AND DAVID M. LESLIE, JR.

United States Fish and Wildlife Service, Oklahoma Ecological Services Field Office, 9014 East 21st Street, Tulsa, OK 74129, USA; [anita\\_barstow@fws.gov](mailto:anita_barstow@fws.gov) (ALB)

United States Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit and Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078-3051, USA; [cleslie@usgs.gov](mailto:cleslie@usgs.gov) (DML)

**Abstract:** *Leopardus braccatus* (Cope, 1889) is a small felid—not much larger than a domestic house cat—commonly called the Pantanal cat. No comprehensive surveys have been conducted to determine how many *L. braccatus* exist in the wild. It is found in humid, warm grasslands and wooded areas of extreme northwestern Argentina, southwestern and south- and north-central (newly reported ranges) Brazil, Paraguay, and Uruguay. Habitat loss and degradation are considered major threats throughout most of its range. It is uncommon in captivity and museum collections, listed with all Felidae under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora, and considered “Near Threatened” by the International Union for Conservation of Nature and Natural Resources in the pampas cat group (= *L. colocolo*).

**Key words:** Argentina, Brazil, *Lynchailurus*, ocelot lineage, *Oncifelis*, pampas cat, Pantanal cat, Paraguay, Uruguay

© 9 April 2012 American Society of Mammalogists  
Synonymies completed 16 January 2012  
DOI: 10.1644/891.1

[www.mammalogy.org](http://www.mammalogy.org)



### *Leopardus* Gray, 1842

*Felis* Linnaeus, 1758:41. Part (*Felis pardalis* Linnaeus, 1758).

*Leopardus* Forskål, 1775:V. Nomen nudum.

*Puma* Jardine, 1834:266. Part (*Puma pajeros*: Jardine, 1834 [= *Felis pajeros* Desmarest, 1816]).

*Leopardus* Gray, 1842:260. Type species *Leopardus griseus* Gray, 1842 (= *Felis pardalis* Linnaeus, 1758), by subsequent designation (Pocock 1917:344, footnote).

*Noctifelis* I. Geoffroy Saint-Hilaire 1844:37. Nomen nudum; not “*Felis à pupille variable*” (vide Kretzoi and Kretzoi 2000:257).

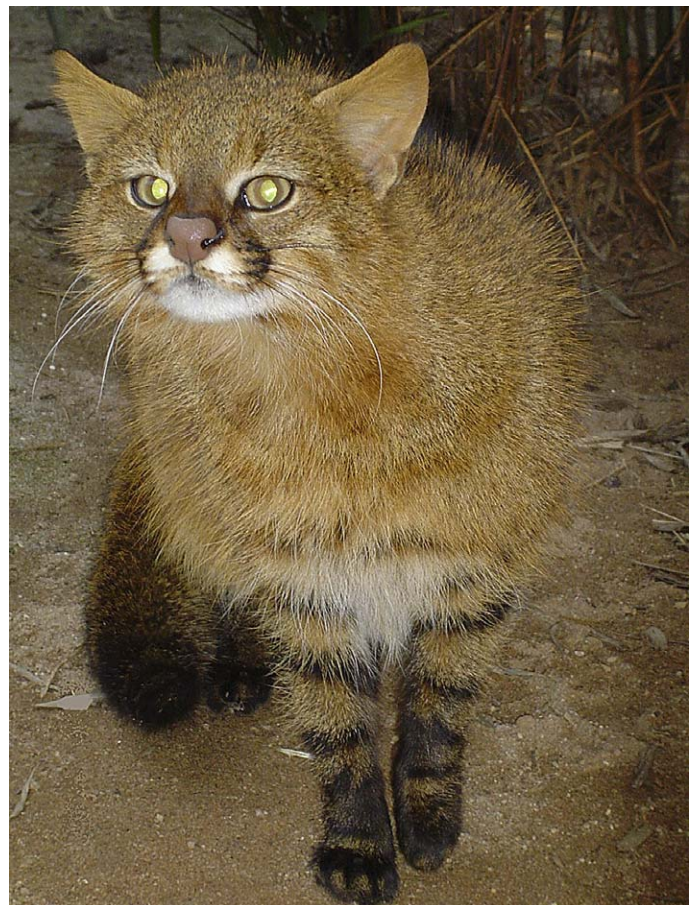
*Oncoides* Severtzov, 1858:386. Type species *Felis pardalis* Linnaeus, 1758, by subsequent designation (Allen 1905:179); proposed as a subgenus of *Felis* Linnaeus, 1758.

*Dendrailurus* Severtzov, 1858:386. Type species *Felis strigilata* Wagner, 1841, by monotypy; proposed as a subgenus of *Felis* Linnaeus, 1758.

*Oncifelis* Severtzov, 1858:386. Type species *Felis geoffroyi* d’Orbigny and Gervais, 1844, by monotypy; proposed as a subgenus of *Felis* Linnaeus, 1758.

→

**Fig. 1.**—*Leopardus braccatus munoai* exhibited as gato palheiro (= *Leopardus colocolo*) at Zoológico del São Paulo. Photograph by Mácia Motta, copyright 2004, available at the Tree of Life Web Project 2010 (<http://tolweb.org/onlinecontributors/app?page=ViewImageData&service=external&sp=29125>, accessed 18 January 2012).



- Noctifelis* Severtzov, 1858:386. Type species *Felis guigna* Molina, 1782, by monotypy; proposed as a subgenus of *Felis* Linnaeus, 1758.
- Lynchailurus* Severtzov, 1858:386. Type species *Felis pajeros* Desmarest, 1816, by monotypy; proposed as a subgenus of *Felis* Linnaeus, 1758.
- Pardalina* Gray, 1867:266. Type species *Pardalina warwickii* Gray, 1867 (= *Felis geoffroyi* d'Orbigny and Gervais, 1844), by monotypy.
- Pajeros* Gray, 1867:269. Type species *Pajeros pampanus* Gray, 1867 (= *Felis pajeros* Desmarest, 1816), by monotypy.
- Pardalis* Gray, 1867:270. Type species *Felis pardalis* Linnaeus, 1758, by absolute tautonymy (Allen, 1919a); proposed as subgenus of *Felis* Linnaeus, 1758.
- Margay* Gray, 1867:271. Type species *Felis macroura* Wied-Neuwied, 1823 (= *Felis wiedii* Schinz, 1821), by subsequent designation (Allen 1916b:580, footnote); proposed as subgenus of *Felis* Linnaeus, 1758.
- Panthera*: Fitzinger, 1869:246, 253, 270, 276. Part (*Panthera tigrinus*: Fitzinger, 1869:246 [= *Felis tigrinus* Schreber, 1775]; *Panthera pardalis*: Fitzinger, 1869:253 [= *Felis pardalis* Linnaeus, 1758]); *Panthera geoffroyi*: Fitzinger, 1869:270 [= *Felis geoffroyi* d'Orbigny and Gervais, 1844]); and *Panthera pajeros*: Fitzinger, 1869 [= *Felis pajeros* Desmarest, 1816]).
- Herpailurus*: Pocock, 1917:346. Part (*Felis geoffroyi* d'Orbigny and Gervais, 1844).
- Oncilla* J. A. Allen, 1919b:358. Type species *Felis pardinoidea oncilla* O. Thomas, 1903, by original designation.
- Mungofelis* Antonius, 1933:13. Type species *Felis braccata* Cope, 1889, by monotypy; proposed as a subgenus of *Felis* Linnaeus, 1758.
- Oreailurus* Cabrera, 1940:16. Type species *Felis jacobita* Cornalia, 1865, by original designation.
- Pseudolynx*: Schwangart, 1941:36. Type species *Lynchailurus (Pseudolynx) kriegi* Schwangart, 1941, by original designation; proposed as a subgenus of *Lynchailurus* Severtzov, 1858; preoccupied by *Pseudolynx* Girault, 1916 (Hymenoptera).
- Montifelis* Schwangart, 1941:37. Type species *Felis colocola* Molina, 1782, by original designation.
- Colocolo* Pocock, 1941:269. Type species *Felis colocola*: Pocock, 1941 (= *Felis jacobita* Cornalia, 1865; not *Felis colocola* Molina, 1782), by original designation.
- Severtzowicus* Kretzoi and Kretzoi, 2000:375. Junior objective synonym of *Noctifelis* Severtzov, 1858; proposed as a replacement name for *Noctifelis* Severtzov, 1858 under the mistaken assumption that *Noctifelis* Severtzov was preoccupied by *Noctifelis* Geoffroy Saint-Hilaire, 1844.

CONTEXT AND CONTENT. Order Carnivora, suborder Feliformia, family Felidae, subfamily Felinae. The relationships

within this genus are controversial and currently in flux (see species' "Context and Content" for relationships as they pertain to this species). We have chosen to follow Wozencraft (2005), who listed 9 species (*braccatus*, *colocolo*, *geoffroyi*, *guigna*, *jacobitus*, *pajeros*, *pardalis*, *tigrinus*, and *wiedii*) under *Leopardus*.

### *Leopardus braccatus* (Cope, 1889) Pantanal Cat

- Felis braccata* Cope, 1889:144. Type locality "province of Rio Grande do Sul, or in Matto Grosso," Brazil; restricted to "Chapada, Matto Grosso" by J. A. Allen (1919b:378).
- Lynchailurus pajeros braccatus*: J. A. Allen, 1919b:376. Name combination.
- Felis (Mungofelis) braccatus*: Antonius 1933:13. Name combination.
- Lynchailurus colocolus braccatus*: Cabrera 1940:12. Name combination.
- Felis colocola muñoai* Ximenez, 1961:1. Type locality "Uruguay."
- Leopardus braccatus*: Wozencraft, 2005:537. First use of current name combination.

CONTEXT AND CONTENT. Context as for genus. Taxonomy of South American small felids has been in flux for at least the past several decades. They have been classified under various genera (e.g., *Felis*, *Leopardus*, *Lynchailurus*, and *Oncifelis*) and have been split into separate species (e.g., Garcia-Perea 1994; Wozencraft 2005), often monotypically, or lumped with various combinations of subspecies (e.g., Sunquist and Sunquist 2002, 2009). Relatively recent molecular evidence (Cossíos et al. 2007, 2009; Johnson et al. 1996, 1999, 2006; Johnson and O'Brien 1997; Masuda et al. 1996; Mattern and McLennan 2000; O'Brien and Johnson 2007; O'Brien and Yuhki 1999; Pecon-Slattey and O'Brien 1998) suggests a phylogeny favoring various subspecific designations, in contrast to systematic conclusions based on just morphological characteristics that suggest unique species (Garcia-Perea 1994).

Using morphological characteristics, Garcia-Perea (1994) assessed the taxonomy of some South American small felids, formerly grouped under *Felis colocolo*, with 86 specimens from Argentina, Brazil, Chile, Ecuador, Paraguay, Peru, and Uruguay, consisting of 72 study skins and 51 skulls, from 8 North American, South American, and European collections. She grouped them under *Lynchailurus* into 3 species: *braccatus* (with the 2 subspecies above; Fig. 1), *pajeros* (7 subspecies), and *colocolo* (2 subspecies).

The size of the ectotympanic bone relative to caudal entotympanic bone of *Leopardus* is usually consistent within species, but some variation in the inflation of the posterior



chamber may be seen among species (Garcia-Perea 1994). Two to 5 distinguishing characteristics of the skulls (e.g., bullar region, orbital region, palatal region, and neurocranium) and teeth were found among the various specimens of *Leopardus*, designated collectively as “pampas cats” (Garcia-Perea 1994). Small felids generally show a great deal of variation in coat patterns and colors. Considering all metrics, as well as geographic affinities, Garcia-Perea (1994) classified 3 “types” of pampas cats and concluded that *colocolo* should be split into 3 species (*braccatus*, *colocolo*, and *pajeros*) with which Wozencraft (2005) concurred. Sunquist and Sunquist (2009:146) formally considered *braccatus* to be 1 of 8 subspecies of *L. colocolo*, but they noted that “*braccatus* and *pajeros* likely represent distinct species.” Most recently, Nascimento (2010), in his unpublished dissertation, identified 16 species of *Leopardus* based on 29 cranial measurements and 14 additional morphological traits from 591 museum specimens; he elevated *L. braccatus munoai* to a full species. Conservation of South American small cats may be the most significant and pressing reason to consider their populations unique enough for special recognition and action (Johnson et al. 1999).

Here, we followed Wozencraft (2005), who listed 2 subspecies of *braccatus*:

*L. b. braccatus* (Cope, 1889). See above.

*L. b. munoai* Ximenez, 1961. See above.

**NOMENCLATURE NOTES.** The etymology of *Leopardus braccatus* is Latin meaning lion–panther and wearing breeches. Common names of *L. braccatus* include Pantanal cat, gato palheiro (Garcia-Perea 1994), and bush cat (Miller 1930).

## DIAGNOSIS

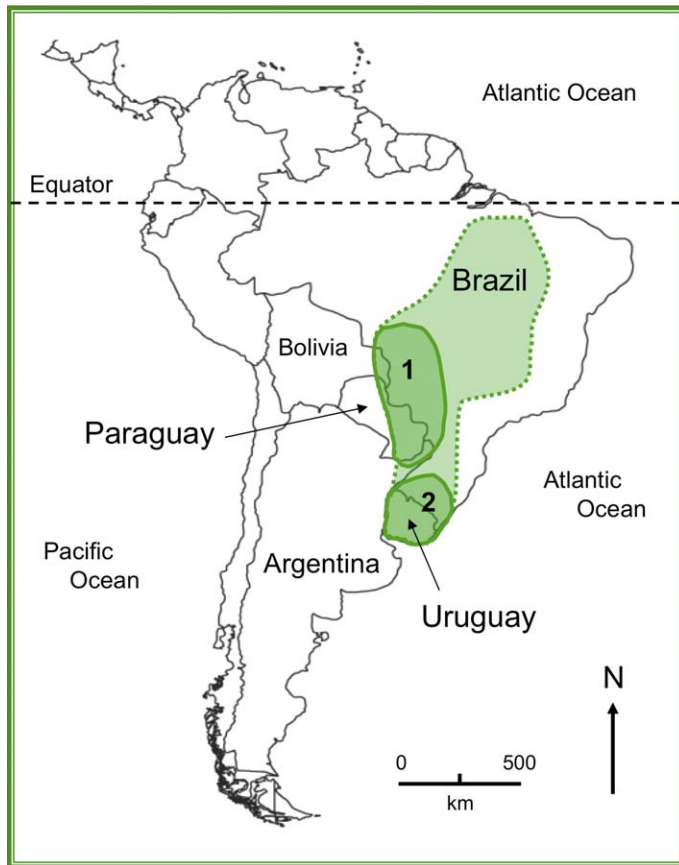
The ectotympanic bone of *Leopardus braccatus* lacks significant posteroventral expansion or inflation and represents only 20–25% of the bullar volume, in contrast to the *colocolo*, *L. colocolo* (40–50%), and the pampas cat, *L. pajeros* (25–35%—Garcia-Perea 1994). Shape of the notch for the postpalatine vein in the palate is “narrow and deep” in *L. braccatus* and “wide and comparatively shallow” in *L. colocolo* and *L. pajeros* (Garcia-Perea 1994:11). The frequency of the presence of P2 is higher in *L. braccatus* (63%,  $n = 8$ ) than in *L. colocolo* (33%,  $n = 6$ ) and *L. pajeros* (0%,  $n = 21$ ). Shape of the main cusp (paracone) of *L. braccatus* is “short and wide in lateral aspect, lacking the sharp appearance” seen in *L. colocolo* and *L. pajeros* (Garcia-Perea 1994:15). The anterior cusp (parastyle) of P3 tends to be absent in all felids except big cats (Salles 1992); however, Garcia-Perea (1994) noted its presence in 3 specimens that she classified as *L. braccatus* and its absence in *L. colocolo* and *L. pajeros*. Lingual tubercles on c1 occur with the highest frequency in *L. braccatus* and at very low frequency in *L. pajeros*; they are absent in *L. colocolo* (Garcia-Perea 1994).

## GENERAL CHARACTERS

Garcia-Perea (1994) describes all species in the “pampas cat” group, including *Leopardus braccatus*, as follows: face has 2 transverse brown to black lines that cross each cheek; superior line starts in the external corner of the eye; inferior line is almost parallel running up around the lateral side of the cheeks; and a 3rd line appears in some specimens at the dorsal end of the inferior line coming from under the chin and throat, creating a sharp angle where the 2 meet on the lateroposterior side of the cheeks. Underside of the chin is white; throat is the same color as the basic coat color, or is somewhat lighter orangish brown, and has 2 or 3 brown stripes that originate on 1 side of the neck and run under the throat to the other side. There are reports of melanistic “pampas cats” in captivity, but a camera-trap photo in Emas Park, Goiás State, Brazil, seems to be the only known record in the wild (Silveira 2005).

There are 2 types of pelage in *L. braccatus*. The 1st type is “almost uniform brown agouti color dorsally” with traces of “dark brown rosettes on flanks” and is characteristic of *L. b. braccatus* (Garcia-Perea 1994:19; [http://www.catsg.org/catsgportal/project-o-month/02\\_webarchive/grafics/sept2005.pdf](http://www.catsg.org/catsgportal/project-o-month/02_webarchive/grafics/sept2005.pdf), accessed 18 January 2012). The spinal crest of *L. b. braccatus* is a little darker than the basic pelage; tail is not ringed but has 2 or 3 lines that do not completely circumvent the tail above a black tip. There are at least 2 (but can be as many as 4) heavy black stripes that wrap around the front legs, and similar stripes on the hind legs, although those stripes may not completely meet on the anterior part of the leg. Spotted ventral markings of *L. b. braccatus* are black; throat is white, grading into orange behind the 1st throat stripe; feet are black dorsally and ventrally, including wrists and ankles, giving the distinctive appearance of wearing boots (Allen 1919b; Garcia-Perea 1994; Miller 1930; Pocock 1941). The 2nd pelage type, typical of *L. b. munoai*, has a background color that is paler and more yellow to orangish on the back and flanks (Fig. 1). Brown spots on flanks are more noticeable than in *L. b. braccatus*, and the feet are black only on palmar and plantar surfaces. The tail of both subspecies is variously tipped in black. In contrast to *L. b. braccatus*, the black tip of *L. b. munoai* is reduced, and the tail itself has only a few discontinuous rings (Garcia-Perea 1994).

Ears of *Leopardus* are large and pointed rather than rounded as in other South American small felids (Silveira 1995); they are usually black on the anterior one-half and gray on the rest of the surface (Silveira 1995); and sometimes there is a pale spot toward the tip of the posterior surface of the ear. The hairs are longer on *L. braccatus* than on other South American species of *Leopardus*. Head–body length of *Leopardus*, in general, is 423–750 mm; tail length is 220–330 mm; and mass is 2.9–3.7 kg (Garcia-Perea 1994; Nowell and Jackson 1996; Redford and Eisenberg 1992; Silveria 1995; Sunquist and Sunquist 2002).



**Fig. 2.**—Known distribution of 1, *Leopardus braccatus braccatus* and 2, *L. b. munoai* in dark green (Garcia-Perea 1994) and the likely expanded range of the species in lighter green, based on recent observations (Bagno et al. 2004; Chebez et al. 2008; de Oliveira 2006; Sánchez-Soto 2007; Silveira 2005).

A dorsal crest is distinctive of the pampas cat group, in which hairs are longer (7 cm) than elsewhere on the body and flanks (1–3 cm—Allen 1919b; Nowell and Jackson 1996). The crest is about 3 cm wide and runs from the back of the neck to the base of the tail; it is reduced in some specimens of *L. braccatus*, making it rather inconspicuous (Courtenay 2002). Both (nonmelanistic) pelage types have 3 or 4 dark brown, almost black, stripes that circumvent the legs, but they may be incomplete on the inner side of the back legs.

## DISTRIBUTION

*Leopardus braccatus* inhabits humid, wet, and warm grasslands and forests of moderate elevation in central South America (Garcia-Perea 1994; Seidensticker and Lumpkin 2004). Two geographically disjunct populations are known to occur east of the Andes (Fig. 2): 1 population in Brazil, Paraguay, and extreme northeastern Argentina (*L. b. braccatus*) and the other population in Uruguay and Rio Grande do Sul, Brazil (*L. b. munoai*—Cáceres et al. 2008;

Garcia-Perea 1994; Nowell and Jackson 1996; Redford and Eisenberg 1992; Sunquist and Sunquist 2009; Ximenez 1961).

Because of its extensive range, *L. b. braccatus* occurs in many more habitat types than *L. b. munoai*. A cat matching Garcia-Perea's (1994) description of *L. b. braccatus* was livetrapped in Minas Gerais, Brazil, except the feet were only black on the palmar and plantar surfaces instead of having the characteristic boot pattern. The Wild Cats of Brazil Project, or Projeto Gatos de Mato-Brasil (de Oliveira 2005, 2006; <http://www.wildcatconservation.org/Wild-Cats-of-Brazil.html>, accessed 26 September 2011) also found camera-trap evidence of *L. b. braccatus* from Maranhão State of northern Brazil; Sánchez-Soto (2007) recorded a road-killed specimen in Mato Grosso do Sul, Brazil; and Chebez et al. (2008) documented its presence in Argentina—all greatly expanding the known range of this subspecies (Bagno et al. 2004; Chebez et al. 2008; de Oliveira 2006; Garcia-Perea 1994; Sánchez-Soto 2007; Silveira 2005). Therefore, the approximate range of *L. b. braccatus* is between 2°S and 22°S and 45°W and 61°W (Fig. 2). *L. b. munoai* occurs only in Uruguay and the state of Rio Grande do Sul, Brazil. Its primary habitat is savanna that occurs from sea level to 514 m above mean sea level (Bagno et al. 2004; Chebez et al. 2008; de Oliveira 2006; Garcia-Perea 1994).

## FOSSIL RECORD

The formation of the Panamanian land bridge permitted endemic small felids of North and Central America to disperse extensively into South America (Eizirik et al. 1998; Johnson et al. 1996; Johnson and O'Brien 1997; O'Brien and Yuhki 1999; Pecon-Slattery et al. 1994; Seidensticker and Lumpkin 2004; Wayne et al. 1989). The land bridge was completely established about 3 million years ago (Coates and Obando 1996), but sea-level changes interrupted its formation several times until the mid-Pleistocene (Beu 2001), suggesting that felid speciation also occurred in South America and recent diversity could be explained by a minimum of 5 or 6 immigrations (Prevosti 2006).

Nine of the 10 Neotropical small felids are in a monophyletic group known as the ocelot lineage (Collier and O'Brien 1985; Eizirik et al. 1998; Johnson et al. 1999; Mattern and McLennan 2000; Pecon-Slattery et al. 1994; Salles 1992). The fossil record of the ocelot lineage is very fragmentary, but specimens are known from the Ensenadan Age 2–0.5 million years ago (Berta 1983; Prevosti 2006). "*Felis*" *vorohuensi* from Buenos Aires Province, Argentina, was described by Berta (1983) and considered Plio-Pleistocene in age. Prevosti (2006) restricted the age of this fossil to 0.78–0.5 million years ago after reexamination of biostratigraphic and chronostratigraphic data from the locality.

The oldest fossils of *Leopardus colocolo* are from late Ensenadan (0.78–0.5 million years ago) and Bonaerian–



**Fig. 3.**—Lateral views of skull (top) and mandible (bottom) and broken piece of premaxillae–nasal and partial orbit (inset) of male *Leopardus braccatus*; United States National Museum of Natural History, specimen 256127, labeled *Oncifelis colocolo braccata*, locality “Brazil: Mato Grosso, Descalvados, Upper Paraguay River,” collected by F. W. Miller, 29 November 1925 (see Miller 1930).

Lujanian (0.5 million–8.5 thousand years ago) localities in the Pampean region of Argentina (Prevosti 2006). A fossil of *L. colocolo* also was found in Tierra del Fuego, Chile, an island not currently inhabited by felids, and thought to be as young as the late Pleistocene or early Holocene (Prevosti 2006). *L. colocolo* split from the common ocelot ancestor about 1.7 million years ago, based on molecular estimates (Johnson et al. 1999). A fossilized left humerus identified as *L. braccatus* from the late Pleistocene–early Holocene recently was found in Serra da Bodoquena, Mato Grosso do Sul, Brazil, near the type locality (Perini et al. 2009).

### FORM AND FUNCTION

*Leopardus braccatus* has retractable claws that are large, compressed, sharp, and strongly curved (Nowak 1991) and digitigrade adaptations of the feet (Flynn et al. 1988). Except for the pads, hairs occur on the feet that allow it to silently stalk prey (Nowak 1991). Ears are large in relationship to head and forward facing, but they can be rotated slightly. Eyes face forward with binocular vision for sharp visual acuity (Flynn et al. 1988); pupils of the eyes adduct creating a vertical slit. The tongue is covered with sharp-pointed, backward-facing, calcified papillae (Flynn et al. 1988) used for lacerating and retaining food within the mouth and for grooming.

The skull is rounded and shortened anteriorly (Fig. 3). Published skull measurements of *L. braccatus* are very

limited, but in the 2 populations that Garcia-Perea (1994:table 4) classified as *braccatus*, ranges (mm) were: greatest length of skull, 94.3–100.5 (4 males); condylobasal length, 89.4–91.8 (4 males); rostral width across the canines, 21.6–24.1 (4 males); mastoidal width, 39.2–42.9 (4 males); interorbital width, 17.2–18.3 (4 males); postorbital width, 27.4–29.7 (3 males); zygomatic width, 62.1–67.5 (4 males and 1 female); length of P4 at the cingulum, 11–13 (4 males and 1 female); and mandibular length, 58.8–63.8 (4 males and 1 female). Dentition reflects the highly predatory lifestyle of an obligate carnivore. The dental formula of *L. braccatus* is  $i\ 3/3, c\ 1/1, p\ 3/2, m\ 1/1$ , total 30 (Garcia-Perea 1994; Nowak 1991).

### ECOLOGY

**Population characteristics.**—There has been limited research on the ecology of *Leopardus braccatus*, so aspects of its ecology and behavior are inferred here from reports on the “pampas cat” group in general (Bagno et al. 2004; Chebez et al. 2008; Cossíos et al. 2007, 2009; Eizirik et al. 1998; Garcia-Perea 1994; Johnson and O’Brien 1997; Johnson et al. 1999; Masuda et al. 1996; Mattern and McLennan 2000; Napolitano et al. 2008; Nowell and Jackson 1996; O’Brien and Yuhki 1999; Pecon-Slattery et al. 1994, 2000, 2004; Pecon-Slattery and O’Brien 1998; Silveira 2005). Longevity ranges from an average of 9 years in the wild up to 16.5 years in captivity (Nowell and Jackson 1996). Litter size is 1–3 kittens, and a captive female gave birth at 24 months of age (Nowell and Jackson 1996; Redford and Eisenberg 1992). Gestation is 80–85 days (Golden 2003).

**Space use.**—Home-range size of *Leopardus braccatus* was 3.07–36.98 km<sup>2</sup> ( $SD = 23.33\ km^2$ ) in Brazilian grasslands (Silveira 2005). Individual pampas cats appeared to be diurnal with some crepuscular and only occasional nocturnal activity (Cabrera and Yepes 1960). Radiotracking studies by Silveira (2005:4) found “virtually no activity during night time.” Vocalizations of *L. braccatus* are similar to other small felids and include meow, growl, spit, hiss, gurgle, and purr (Sunquist and Sunquist 2002).

*Leopardus braccatus* is known to occur in many biomes in South America including the Pantanal, Chaco, Pampas, Cerrado, Espinal, Monte, deciduous forests, and transitional areas, all found in Argentina, Brazil, Paraguay, and Uruguay. These habitats are being rapidly converted from native vegetation to cattle ranching and agricultural fields, and severe fragmentation by roads and urban sprawl are growing problems throughout the range of *L. braccatus* (Bagno et al. 2004; Cavalcanti and Gese 2009; Soisalo and Cavalcanti 2006; Trolle 2003). *L. braccatus* is reportedly found in pastures and agricultural fields, demonstrating that it can use human-altered habitats (Bagno et al. 2004) and adapt to changing environments. Within the range of *L. b. mumoi* in Uruguay and southern Brazil, the Paraguay and

Rio de la Plata river basins are believed to be barriers to dispersal and gene flow (Johnson et al. 1999).

*Leopardus braccatus* occupies humid and warm grasslands and forests from sea level to 2,000 m (Garcia-Perea 1994; Johnson et al. 1999). Annual rainfall varies within the range of *L. braccatus* because it occurs in a wide variety of ecotypes: Chaco (dry forests and wet savannas), annual rainfall 450–1,200 mm (increasing from west to east), winter–summer temperatures 20–23°C; Espinal (xerophitic forests), annual rainfall 400–1,000 mm (increasing from south to north), winter–summer temperatures 15–20°C; and Monte (dry shrub–scrub steppe), annual rainfall 80–200 mm, winter–summer temperatures 13–17°C (Bagno et al. 2004). The vegetation within the range of *L. braccatus* is generally characterized by a mix of open grasslands to dense woodlands.

Seasonal precipitation, soil fertility, drainage, fire regime, and climatic fluctuations influence development of the different vegetative stages within the range of *L. braccatus* (Bagno et al. 2004; de Oliveira-Filho and Ratter 2002; Trolle 2003). Along the transitional zone from grassland to woodland, various vegetative stages have been described. The stages of transition are campo limpo (clean field), a grassland with no shrubs or trees; campo sujo (dirty field), a grassland with a scattering of small trees and shrubs; campo cerrado (closed field), with tree cover of 30–90%; and cerradão (dense woodland), the last stage almost completely covered with large trees and sparse ground-cover layer.

*Leopardus braccatus* gets its common name, Pantanal cat, from the Pantanal wetland complex, a 140,000-km<sup>2</sup> floodplain of the Paraña–Paraguay watersheds. The Pantanal is typified by a mosaic of the major biomes of central Brazil, Paraguayan Chaco, and Amazonian forest; a matrix of open fields interspersed with isolated patches of secondary forests and gallery forests border intermittent and permanent rivers (Cavalcanti and Gese 2009). The Pantanal is almost totally inundated during the rainy season in October–March, with mean monthly precipitation of 145 mm; during the dry season in April–September, its mean monthly precipitation is only 48 mm. Climate is seasonal, with warm, wet summers and cold, dry winters; winter–summer temperatures are 18–42°C (Cavalcanti and Gese 2009; Trolle 2003).

When the Pantanal is not seasonally flooded, many small water depressions are dispersed throughout its grasslands or forests. *L. braccatus* can be found among clumps of tall pampas grass in Uruguay and in low-lying swampy areas (Nowell and Jackson 1996; Silveira 1995; Ximenez 1961). *L. braccatus* has recently been found much farther north than previously recorded (de Oliveira 2005, 2006), and rates of land conversion and fragmentation of available habitat in the Pantanal are increasing (Cavalcanti and Gese 2009), perhaps putting pressure on *L. braccatus* to seek out alternative habitats.

**Diet.**—*Leopardus braccatus* appears to feed on ground birds, small mammals, and guinea pigs (*Cavia aperea*—Nowell and Jackson 1996; Silveira 1995). Stomach contents of 4 recent road-killed individuals contained small lizards and a colubrid snake (Colubridae)—the 1st record of reptiles in the diet of *L. braccatus*. Plant material, some beetles, and a small diurnal–crepuscular rodent also were found in the stomachs, suggesting nocturnal and diurnal activity of *L. braccatus* (Bagno et al. 2004).

**Diseases and parasites.**—No specific diseases have been reported for *Leopardus braccatus*, but *Toxoplasma gondii*, a parasitic protozoan responsible for toxoplasmosis in humans, was reported in a captive *Oncifelis* (= *Leopardus*) *colocolo* in Brazil. Little is known about what role wild felids have in the natural epidemiology of *T. gondii*, or as a cause of felid mortality or morbidity (Silva et al. 2001). Two captive *Oncifelis* (= *Leopardus*) *colocolo* in North American zoos had active feline leukemia virus, and other captive Brazilian pampas cats tested positive for the virus (Filoni et al. 2003). Feline immunodeficiency virus and antibodies to feline coronavirus were reported in captive Brazilian felids including *Oncifelis* (= *Leopardus*) *colocolo* (Filoni et al. 2006). Antibodies of *Bartonella henselae* (a proteobacterium) were found at very high prevalence in free-ranging Brazilian felids, implying the cats act as a reservoir. *B. henselae* causes cat scratch disease in humans; fleas and ticks in the genus *Ixodes* may serve as potential vectors for its transmission (Filoni et al. 2006).

Ticks (Acari: Ixodida) that occur primarily on horses and cattle also occur on carnivores in areas where the original vegetation has been replaced with cultivated pastures and are affected by other anthropogenic disturbances and fragmentation (Labruna et al. 2005). Fungal dermatophytes that can lead to parasitic skin infections and cause superficial mycoses in animals and humans have been found in asymptomatic healthy wild felids in captivity at Fundação Parque Zoológico de São Paulo, Brazil. Samples were taken from 130 adult animals of both sexes, including large, medium, and small cats; specifically, 8 *Oncifelis* (= *Leopardus*) *colocolo* were confirmed as asymptomatic carriers and sources of potential infection for other animals and humans (Bentubo et al. 2006). Many captive small felid species show some degree of skin disorders, traumatic lesions, enteritis, and dental disorders (Filoni et al. 2003).

**Interspecific interactions.**—*Leopardus braccatus* is sympatric with other small felids such as *L. tigrinus* (oncilla or little tiger cat) and *L. geoffroyi* (Geoffroy's cat—Bagno et al. 2004; Hemmer 1978; Johnson et al. 1999; Silveira 2005). *L. braccatus* hybridized with *L. tigrinus* in areas of range overlap (Cossios et al. 2009; Johnson et al. 1999). Jaguars (*Panthera onca*) are known to inhabit areas of the Pantanal in Argentina (Soisalo and Cavalcanti 2006), and landscape-level surveys in eastern Paraguay revealed that small spotted cats such as *L. braccatus* avoid areas where jaguars occur (Zuercher et al. 2001).



## GENETICS

The genus *Leopardus* has a reduced number of diploid chromosomes ( $2n = 36$ ), unlike other cat genera that have 38 chromosome pairs (Collier and O'Brien 1985; Hemmer 1978; Mattern and McLennan 2000; Wayne et al. 1989). The unique metacentric chromosome, C3, in *Leopardus* results from the fusion of 2 acrocentric F-group chromosomes.

Over the last decade, O'Brien and colleagues performed genetic analyses on various aspects of the "pampas cat" genome (including but not limited to *Leopardus braccatus*), such as phylogenetic reconstruction, gene sequencing of both nuclear and mitochondrial DNA, and protein electrophoresis (Cossíos et al. 2009; Eizirik et al. 1998; Johnson and O'Brien 1997; Johnson et al. 1999; Masuda et al. 1996; Mattern and McLennan 2000; Napolitano et al. 2008; O'Brien and Yuhki 1999; Pecon-Slattey et al. 1994, 2000, 2004; Pecon-Slattey and O'Brien 1998). Contrary to Wozencraft (2005) and the suggestions of Sunquist and Sunquist (2009), those molecular studies suggested that all species split by Garcia-Perea (1994) should be subspecies under *L. colocolo*. Although O'Brien and colleagues maintained confidence in the origins and blood lines of the samples collected and subsequently used in most genetic studies of *L. colocolo* (S. J. O'Brien, pers. comm., 2010), many of these samples were not collected from wild-caught individuals, but rather most samples were collected from individuals in various zoos; some with unknown histories or origins. This introduces some degree of uncertainty in taxonomic conclusions to date.

Genetic studies by Johnson et al. (1999) identified hybrids in the general area of home-range overlap between a male *L. braccatus* and a female *L. tigrinus*; the hybrids displayed the tigrina pelage. Trigo et al. (2008) performed further genetic investigations with an expanded data set and found more of the same hybridizations. One animal tested by Trigo et al. (2008) was believed to be a hybrid in the opposite direction (mitochondrial DNA from *L. tigrinus* introgressed into a *L. colocolo*) documenting additional crossbreeding within the group; however, the origin and "race" of that animal was unknown. Naturally occurring hybrids may come from areas of distributional overlap, and such individuals may exhibit morphological problems such as unusual penile structure and lack of spermatozoa in ejaculate, as was found in 1 adult male hybrid (Johnson et al. 1999).

## CONSERVATION

In Brazil and Argentina, *Leopardus braccatus* is considered "Vulnerable." The International Union for Conservation of Nature and Natural Resources lists the pampas cat group (= *L. colocolo*) as "Near Threatened" (Pereira et al. 2008) because future population declines are likely to result from land conversion of native habitat to agricultural crops,

land degradation from cattle grazing, fragmentation, hunting by local farmers in retaliation for depredation of their chickens, and decline of prey populations (Bagno et al. 2004; Cossíos et al. 2009; Soisalo and Cavalcanti 2006; Trolle 2003). Grazing in the Pantanal has been shown to have adverse impacts on the environment; more specifically, forests in the Pantanal are now dominated by invasive Acurí palms (*Attalea phalerata*) with little undergrowth and relatively little woody plant species (Trolle 2003).

For conservation of *L. braccatus* to be effective, more-specific information is needed about its distribution, population status, ecological requirements, and genetic diversity (Lucherini et al. 2004). Methods to monitor important habitats of *L. braccatus* will continue to include camera-trapping (Trolle 2003), because the species is recognizable from its coat pattern (Lucherini et al. 2004). Studies have shown genetic differences in alleles of *L. braccatus* and other closely related *Leopardus* species (Johnson et al. 1999; Trigo et al. 2008), but more basic research is needed on the systematics of South American small cats in general due to conflicting results from molecular and morphological studies (Sunquist and Sunquist 2009).

During the Miocene, the climate of Earth changed, resulting in pronounced ecological shifts in habitat characteristics and availability. As parts of South America became more arid and seasonal, the shrub-grassland steppe initially appeared as a continuum of habitats that changed from dense forests to open expanses. Species no doubt adapted to these changes, but populations likely became isolated as preferred habitats became more disjunct. Some species, such as *L. braccatus*, probably started to exploit newly developing shrublands and grasslands, which provided novel prey (Canepuccia et al. 2008; Hemmer 1979).

Amid current changes in global climate, precipitation regimes will become altered, and effects of habitat change on species abundance and biodiversity will be amplified, likely increasing emigration and adversely impacting survival rates at the population level (Canepuccia et al. 2008; Hemmer 1979). Areas in Argentina within the current range of *L. braccatus* have experienced an increase in annual precipitation of 10–30% over the last 50 years (Canepuccia et al. 2008). *L. braccatus* may face greater threats in low-lying areas with increased precipitation, given that most native uplands have been converted to agriculture (as much as 80% of the Cerrado—Bagno et al. 2004) and are used for grazing. These effects can adversely impact populations, both directly and indirectly, by altering fitness and modifying availability of resources. Prey abundance may be reduced, and den sites may be lost to flooding. These interactions suggest that global climatic patterns could have significant negative impacts at regional and local population scales (Canepuccia et al. 2008).

To foster the conservation of *L. braccatus*, the following actions might be beneficial: reduce loss of native habitat to



agriculture; identify populations and metapopulations of *L. braccatus* across its entire range; create conservation areas to minimize further habitat loss and public outreach programs to educate people about the species and its needs; and generally increase awareness of the vulnerability of all species in this part of South America. Furthermore, additional genetic research on wild-caught individuals could help validate or refute earlier genetic research performed on largely captive animals.

### ACKNOWLEDGMENTS

We thank C. A. Davis, J. H. Shaw, and Z. Roehrs for reviewing drafts of this account and J. P. Jorgenson, Division of Scientific Authority, United States Fish and Wildlife Service, for help with establishing contacts with felid researchers in South America. T. de Oliveira provided support and encouragement for this effort. Logistical and financial support was provided by the United States Fish and Wildlife Service's Oklahoma Ecological Services Field Office and the Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma State University, Oklahoma Department of Wildlife Conservation, United States Geological Survey, United States Fish and Wildlife Service, and Wildlife Management Institute, cooperating). The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the United States Fish and Wildlife Service or the United States Geological Survey.

### LITERATURE CITED

- ALLEN, J. A. 1905. Reports of the Princeton University expeditions to Patagonia, 1896–1899. Vol. 3. Zoölogy. Part 1. Mammalia of southern Patagonia. J. Pierpoint Morgan Fund, Princeton University, Princeton, New Jersey, and Schweizerbart'sche Verlagshandlung, Stuttgart, Germany.
- ALLEN, J. A. 1919a. Severtzov's classification of the Felidae. *Bulletin of the American Museum of Natural History* 41:335–340.
- ALLEN, J. A. 1919b. Notes on the synonymy and nomenclature of the smaller spotted cats of tropical America. *Bulletin of the American Museum of Natural History* 41:341–419.
- ANTONIUS, W. VON O. 1933. Über *Felis braccata* Cope und andere Schönbrunner Kleinkatzen. *Der Zoologische Garten* 6:10–22.
- BAGNO, M. A., ET AL. 2004. Notes on the natural history and conservation status of pampas cat, *Oncifelis colocolo*, in the Brazilian Cerrado. *Mammalia* 68:75–79.
- BENTUBO, H. D. L., ET AL. 2006. Isolation of *Microsporium gypseum* from the haircoat of healthy wild felids kept in captivity in Brazil. *Journal of Microbiology* 37:148–152.
- BERTA, A. 1983. A new species of small cat (Felidae) from the late Pliocene–early Pleistocene (Uquian) of Argentina. *Journal of Mammalogy* 64:720–725.
- BEU, A. G. 2001. Gradual Miocene to Pleistocene uplift of the Central American Isthmus: evidence from tropical American Tonnoidean gastropods. *Journal of Paleontology* 75:706–720.
- CABRERA, A. 1940. Notas sobre carnívoros sudamericanos. *Notas del Museo de La Plata Zoología* 5(29):1–22.
- CABRERA, A., AND J. YEPES. 1960. Mamíferos Sud-Americanos, vida, costumbres y descripción. *Historia Natural Ediar*, Buenos Aires 2:159–370.
- CÁCERES, N. C., A. P. CARMIGNOTTO, E. FISCHER, AND C. F. SANTOS. 2008. Mammals from Mato Grosso do Sul, Brazil; lists of species. *Journal of Species Lists and Distribution*, Check List 4:321–335.
- CANEPUCCIA, A. D., A. A. FARIAS, A. H. ESCALANTE, O. IRIBARNE, A. NOVARO, AND J. P. ISACCH. 2008. Differential response of marsh predators to rainfall-induced habitat loss and subsequent variations in prey availability. *Canadian Journal of Zoology* 86:407–418.
- CAVALCANTI, S. M. C., AND E. M. GESE. 2009. Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy* 90:935–945.
- CHEBEZ, J. C., N. A. NIGRO, G. A. SOLÍS, AND A. T. STRUMIA. 2008. Confirmación de la presencia del gato del Pantanal *Lynchailurus braccatus* (Cope, 1889) en la Argentina. *Nótulas Faunísticas—Segunda Serie* 19:1–11.
- COATES, A. G., AND J. A. OBANDO. 1996. The geologic evidence of the Central American Isthmus. Pp. 21–56 in *Evolution and environment in tropical America* (B. C. Jackson, A. F. Budd, and A. G. Coates, eds.). University of Chicago Press, Chicago, Illinois.
- COLLIER, G. E., AND S. J. O'BRIEN. 1985. A molecular phylogeny of the Felidae: immunological distance. *Evolution* 39:437–487.
- COPE, E. D. 1889. On the mammalia obtained by the Naturalist Exploring Expedition to southern Brazil. *American Naturalist* 23(266):128–150.
- CORNALIA, E. 1865. Descrizione di una nuova specie del genere: *Felis. Felis jacobita* (Corn.). *Memorie della Società Italiana di Scienze Naturali* 1:1–10.
- COSSÍOS, D., M. LUCHERINI, M. RUIZ-GARCÍA, AND B. ANGERS. 2009. Influence of ancient glacial periods on the Andean fauna: the case of the pampas cat (*Leopardus colocolo*). *BMC Evolutionary Biology* 9:68.
- COSSÍOS, D., ET AL. 2007. Update on the distribution of the Andean cat *Oreailurus jacobita* and the pampas cat *Lynchailurus colocolo* in Peru. *Endangered Species Research* 3:313–320.
- COURTENAY, O. 2002. A new record of pampas cat, *Lynchailurus braccatus*, in Brazil. *Mammalia* 66:295–297.
- DE OLIVEIRA, T. G. 2005. Wild cats of Brazil project/Projeto gatos do mato—Brasil. Cat project of the month—July. International Union for Conservation of Nature and Natural Resources/Species Survival Commission Cat Specialist Group feature project of the month. [www.catsg.org/catsgportal/project-o-month/02\\_webarchive/webarchive.htm](http://www.catsg.org/catsgportal/project-o-month/02_webarchive/webarchive.htm), accessed 26 February 2010.
- DE OLIVEIRA, T. G. 2006. Project wild cats of Brazil. *Wild Cat News* 2(2):1–8.
- DE OLIVEIRA-FILHO, A. T., AND J. A. RATTER. 2002. Vegetation physiognomies and woody flora of the Cerrado biome. Pp. 91–420 in *The Cerrados of Brazil: ecology and natural history of a Neotropical savanna* (P. S. Oliveira and R. J. Marquis, eds.). Columbia University Press, New York.
- DESMAREST, A.-G. 1816. *Chat, Felis*, Linn., Briss., Schreb., Cuv. Pp. 73–123 in *Nouveau dictionnaire d'histoire naturelle, appliqué aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc. Par une société de naturalistes et d'agriculteurs*, Nouv. ed. 6. Deterville, Paris, France.
- D'ORBIGNY, A., AND P. GERVAIS. 1844. *Mammalogie: nouvelle espèce de Felis*. *Extraits des Procès Verbaux Séances, Société Philomathique de Paris* 1844:40–41.
- EIZIRIK, E., ET AL. 1998. Phylogeographic patterns and evolution of the mitochondrial DNA control region in two Neotropical cats (Mammalia, Felidae). *Journal of Molecular Evolution* 47:613–624.
- FILONI, C., C. H. ADANIA, E. L. DURIGON, AND J. L. CATÃO-DIAS. 2003. Serosurvey for feline leukemia virus and lentiviruses in captive small Neotropical felids in São Paulo State, Brazil. *Journal of Zoo and Wildlife Medicine* 34:65–68.
- FILONI, C., ET AL. 2006. First evidence of feline herpesvirus, calicivirus, parvovirus, and *Ehrlichia* exposure in Brazilian free-ranging felids. *Journal of Wildlife Diseases* 42:470–477.
- FITZINGER, L. J. 1869. Revision der zur natürlichen Familie der Katzen (Feles) gehörigen Formen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften* 59:211–279.
- FLYNN, J. E., N. A. NEFF, AND R. H. TEDFORD. 1998. Phylogeny of the Carnivora. Pp. 73–116 in *The phylogeny and classification of the tetrapod* (M. J. Benton, ed.). Vol. 2. Clarendon Press, Oxford, United Kingdom.
- FORSKÅL, P. 1775. *Descriptiones animalium: avium, amphibiorum, piscium, insectorum, vermium; quæ in itinere Orientali (post mortem auctoris Carsten Niebuhr). Mölleri*, Copenhagen, Denmark.
- GARCIA-PEREA, R. 1994. The pampas cat group (genus *Lynchailurus* Severtzov, 1858) (Carnivora: Felidae), a systematic and biogeographic review. *American Museum Novitates* 3096:1–35.

- GEOFFROY SAINT-HILAIRE, I. 1844. Voyages dans l'Inde par V. Jacquemont, pendant les années 1828 à 1832. Tome VI. Part 2. Didot Frères, Paris, France.
- GIRAULT, A. 1916. A new genus of Eulophidae from the United States. *Entomological News* 27:152–154.
- GOLDEN, R. 2003. *Leopardus colocolo* (on-line). Animal Diversity Web. [http://animaldiversity.ummz.umich.edu/site/accounts/information/Leopardus\\_colocolo.html](http://animaldiversity.ummz.umich.edu/site/accounts/information/Leopardus_colocolo.html), accessed 20 April 2010.
- GRAY, J. E. 1842. Descriptions of some new genera and fifty unrecorded species of Mammalia. *Annals and Magazine of Natural History, Series 1*, 10:255–267.
- GRAY, J. E. 1867. Notes on the skulls of the cats (Felidae). *Proceedings of the Scientific Meetings of the Zoological Society of London* 1867:258–277.
- HEMMER, H. 1978. The evolutionary systematics of living Felidae: present status and current problems. *Carnivore* 1:71–79.
- HEMMER, H. 1979. Fossil history of the living Felidae. *Carnivore* 2: 58–61.
- JARDINE, W. 1834. The naturalist's library. Vol. 16. Mammalia. Part 2. Felinae. W. H. Lazars, Edinburgh, United Kingdom.
- JOHNSON, W. E., P. A. DRATCH, J. S. MARTENSON, AND J. S. O'BRIEN. 1996. Resolution of recent radiations within three evolutionary lineages of Felidae using mitochondrial restriction fragment length polymorphism variation. *Journal of Mammalian Evolution* 3:97–120.
- JOHNSON, W. E., AND S. J. O'BRIEN. 1997. Phylogenetic reconstruction of the Felidae using 16S rRNA and NADH-5 mitochondrial genes. *Journal of Molecular Evolution* 44, supplement:98–116.
- JOHNSON, W. E., ET AL. 1999. Disparate phylogeographic patterns of molecular genetic variation in four closely related South American small cat species. *Molecular Ecology* 8, supplement: 79–94.
- JOHNSON, W. E., ET AL. 2006. The late Miocene radiation of modern Felidae: a genetic assessment. *Science* 311:73–77.
- JOHNSON, W. E., ET AL. 1999. Disparate phylogeographic patterns of molecular genetic variation in four closely related South American small cat species. *Molecular Ecology* 8, supplement: 79–94.
- KRETZOI, M., AND M. KRETZOI. 2000. *Fossilium catalogus animalia. Index generum et subgenerum mammalium*. Backhuys Publishers, Leiden, The Netherlands.
- LABRUNA, M. B., ET AL. 2005. Ticks (Acari: Ixodida) on wild carnivores in Brazil. *Experimental and Applied Acarology* 36:149–163.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. Impensis Direct Laurentii Salvii, Stockholm, Sweden.
- LINNAEUS, C. 1771. *Mantissa plantarum altera generum editionis VI et specierum II. Impensis Direct Laurentii Salvii, Stockholm, Sweden*.
- LUCHERINI, M., L. SOLER, AND E. L. VIDAL. 2004. A preliminary revision of knowledge status of felids in Argentina. *Mastozoología Neotropical* 11:7–17.
- MASUDA, R., J. V. LOPEZ, J. P. SLATTERY, N. YUHKI, AND S. J. O'BRIEN. 1996. Molecular phylogeny of mitochondrial cytochrome *b* and 12S rRNA sequences in the Felidae: ocelot and domestic cat lineages. *Molecular Phylogenetics and Evolution* 6:351–365.
- MATTERN, M. Y., AND D. A. MCLENNAN. 2000. Phylogeny and speciation of felids. *Cladistics* 16:232–253.
- MILLER, F. W. 1930. Notes on some mammals of southern Matto Grosso, Brazil. *Journal of Mammalogy* 11:10–22.
- MOLINA, G. I. 1782. *Saggio sulla storia naturale de Chili. Nella Stamperia di S. Tommaso d'Aquino, Bologna, Italy*.
- NAPOLITANO, C., ET AL. 2008. Ecological and biogeographical inferences of two sympatric and enigmatic Andean cat species using genetic identification of faecal samples. *Molecular Ecology* 17:678–690.
- NASCIMENTO, F. O. DO. 2010. *Revisão taxonômica do gênero Leopardus Gray, 1842 (Carnivora, Felidae)*. Ph.D. dissertation, Instituto de Biociências da Universidade de São Paulo, São Paulo, Brasil.
- NOWAK, R. M. 1991. *Walker's mammals of the world*. 5th ed. Johns Hopkins University Press, Baltimore, Maryland.
- NOWELL, K., AND P. JACKSON. 1996. *Wild cats: status survey and conservation action plan*. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- O'BRIEN, S. J., AND W. E. JOHNSON. 2007. The evolution of cats. *Scientific American Magazine* July:68–75.
- O'BRIEN, S. J., AND N. YUHKI. 1999. Comparative genome organization of the major histocompatibility complex: lessons from the Felidae. *Immunological Reviews* 167:133–144.
- PECON-SLATTERY, J., W. E. JOHNSON, D. GOLDMAN, AND S. J. O'BRIEN. 1994. Phylogenetic reconstruction of South American felids defined by protein electrophoresis. *Journal of Molecular Evolution* 39:296–305.
- PECON-SLATTERY, J., AND S. J. O'BRIEN. 1998. Patterns of Y and X chromosomes DNA sequences divergence during the Felidae radiation. *Genetics* 148:1245–1255.
- PECON-SLATTERY, J., A. J. PEARKS WILKERSON, W. J. MURPHY, AND S. J. O'BRIEN. 2004. Phylogenetic assessment of introns and SINES within the Y chromosome using the cat family Felidae as a species tree. *Molecular Biology and Evolution* 21:2299–2309.
- PECON-SLATTERY, J., L. SANNER-WACHTER, AND S. J. O'BRIEN. 2000. Novel gene conversion between X–Y homologues located in the non-recombining region of the Y chromosome in Felidae (Mammalia). *Proceedings of the National Academy of Sciences* 97:5307–5312.
- PEREIRA, J., M. LUCHERINI, T. DE OLIVEIRA, E. EIZIRK, G. ACOSTA, AND R. LEITE-PITTMAN. 2008. *Leopardus colocolo*. International Union for the Conservation of Nature and Natural Resources Red list of threatened species. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland. [www.iucnredlist.org](http://www.iucnredlist.org), accessed 7 September 2011.
- PERINI, F. A., ET AL. 2009. Carnivores (Mammalia, Carnivora) from the Quaternary of Serra da Bodoquena, Mato Grosso do Sul, Brazil. *Arquivos do Museu Nacional, Rio de Janeiro* 67:119–128.
- POCOCK, R. I. 1917. The classification of existing Felidae. *Annals and Magazine of Natural History, Series 8*, 20:329–350.
- POCOCK, R. I. 1941. The examples of the *Colocolo* and of the pampas cat in the British Museum. *Annals and Magazine of Natural History, Series 11*, 7:257–274.
- PREVOSTI, F. J. 2006. New material of Pleistocene cats (Carnivora, Felidae) from southern South America with comments on biogeography and the fossil record. *Geobios* 39:679–694.
- REDFORD, K. H., AND J. F. EISENBERG. 1992. *Mammals of the Neotropics: the southern cone*. University of Chicago Press, Chicago, Illinois.
- SALLES, L. O. 1992. Felid phylogenetics: extant taxa and skull morphology (Felidae, Aeluroidea). *American Museum Novitates* 3047:2–64.
- SÁNCHEZ-SOTO, S. 2007. Nuevo registro de *Oncifelis colocolo* (Felidae) para el Pantanal de Brasil. *Revista Mexicana de Biodiversidad* 78:211–212.
- SCHINZ, H. R. 1821. *Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier*. Ester Band, Säugethiere und Vögel, Stuttgart, Germany.
- SCHREBER, J. C. D. VON. 1775. *Die Säugethiere in Abbildungen nach der Natur, mit Beschreibungen*. Stieffried Leberecht Crusius, Leipzig, Germany.
- SCHWANGART, F. 1941. *Südamerikanische Busch-, Berg- und Steppenkatzen*. Bayerische Akademie der Wissenschaften, Abhandlungen der Mathematisch-naturwissenschaftlichen Klasse, Neue Folge 49:1–44.
- SEIDENSTICKER, J., AND S. LUMPKIN. 2004. *Cats: the Smithsonian answer book*. Smithsonian Institution Press, Washington, D.C.
- SEVERTZOV, M. N. 1858. Notice sur la classification multériale des carnivores, spécialement des félidés, et les études de zoologie générale qui s'y rattachent. *Revue et Magazine de Zoologie* 9:358–393.
- SILVA, J. C. R., ET AL. 2001. Seroprevalence of *Toxoplasma gondii* in captive Neotropical felids from Brazil. *Veterinary Parasitology* 102:217–224.
- SILVEIRA, L. 1995. Notes on the distribution and natural history of the pampas cat, *Felis colocolo*, in Brazil. *Mammalia* 59:284–288.
- SILVEIRA, L. 2005. Carnivore population ecology in Cerrado environment. Jaguar Conservation Fund, Earthwatch Institute, Maynard, Massachusetts.
- SOISALO, M. K., AND S. M. C. CAVALCANTI. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* 129:478–496.
- SUNQUIST, M. E., AND F. C. SUNQUIST. 2002. *Wild cats of the world*. University of Chicago Press, Chicago, Illinois.
- SUNQUIST, M. E., AND F. C. SUNQUIST. 2009. Family Felidae (cats). Pp. 54–169 in *Handbook of the mammals of the world*. Vol. 1.

- Carnivores (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.
- THOMAS, O. 1903. Notes on the Neotropical mammals of the genera *Felis*, *Hapale*, *Oryzomys*, *Akodon*, and *Ctenomys*, with descriptions of new species. *Annals and Magazine of Natural History, Series 7*, 12:234–243.
- TRIGO, T. C., ET AL. 2008. Inter-species hybridization among Neotropical cats of the genus *Leopardus*, and evidence for an introgressive hybrid zone between *L. geoffroyi* and *L. tigrinus* in southern Brazil. *Molecular Ecology* 17:4317–4333.
- TROLLE, M. 2003. Mammal survey in the southeastern Pantanal, Brazil. *Biodiversity and Conservation* 12:823–836.
- WAGNER, J. A. 1841. *Die Säugethiere in Abbildungen nach der nature mit Beschreibungen. Supplementband 2.* Bob'schen, Erlangen, Germany.
- WAYNE, R. K., R. E. BENVENISTE, D. N. JANCZEWSKI, AND S. J. O'BRIEN. 1989. Molecular and biochemical evolution of the Carnivora. Pp. 465–494 in *Carnivore behavior, ecology, and evolution* (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York.
- WIED-NEUWIED, M. 1823. *Abbildungen zur Naturgeschichte von Brasilien.* Verlage des Grossherzoglichen Sächs Landes-Industrie-Comptoirs, Weimar, Germany.
- WOZENCRAFT, W. C. 2005. Order Carnivora. Pp. 532–628 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.
- XIMENEZ, A. 1961. New subspecies of pampas cat from Uruguay, *Felis colocolo muñoai*. *Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo* 88:1–8.
- ZUERCHER, G. L., P. S. GIPSON, AND K. HILL. 2001. A predator–habitat assessment for felids in the inland Atlantic forest of eastern Paraguay: a preliminary analysis. *Endangered Species Update* 18:115–119.
- PAMELA OWEN reviewed the fossil account and SERGIO SOLARI and ALFRED GARDNER reviewed the synonymies. Associate editor and Editor of this account was MEREDITH J. HAMILTON.