

## *Lycalopex gymnocercus* (Carnivora: Canidae)

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**Abstract:** *Lycalopex gymnocercus* (Fischer, 1814) is a canid commonly called the Pampas fox. A sexually dimorphic fox-like carnivore of medium size with reddish coloration on sides and white on the ventral surface, it is 1 of 6 species in the genus *Lycalopex*. It occurs in eastern Bolivia, western and central Paraguay, Uruguay, north and central Argentina, and southeastern Brazil. It prefers open habitats but also occurs in areas of Pampas grassland modified by extensive ranching and agriculture activities. It has been assigned to the “Least Concern” category of the International Union for Conservation of Nature and Natural Resources. DOI: 10.1644/820.1.

**Key words:** canid, grassland, Pampas fox, South America

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### *Lycalopex gymnocercus* (Fischer, 1814) Pampas Fox

*Procyon gymnocercus* Fischer, 1814:178. Based solely on “L’Agourachay” of Azara (1801:317); therefore, type locality is Paraguay, restricted by Cabrera (1958:235) to vicinity of Asunción.

*Canis brasiliensis* Schinz, 1821:220. Type locality “Brasilien and Paraguay.”

*Canis protalopex* Lund, 1840:54, text in plate 28 (figure 9). Type locality “Rio das Velhas,” Lagoa Santa, Minas Gerais, Brazil.

*Canis* [(*Pseudalopex*)] *gracilis* Burmeister, 1861:406. Type locality “die buschige Pampa in den Umgebungen Mendozas,” Mendoza, Argentina.

*Canis patagonicus* Philippi, 1866:116. Type locality “Magellanes Strasse,” Magellanes, Chile.

*Canis azarae*, m. *fossilis* Ameghino, 1889:298. Type locality “Rio Lujan y Cañada de Rocha en los partidos de Mercedes y Lujan, provincia de Buenos Aires,” Argentina.

*Canis azarae*, m. *antiquus* Ameghino, 1889:298. Type locality “Rio Lujan en los partidos de Mercedes y Lujan, provincia de Buenos Aires,” Argentina.

*Canis domeykoanus* Philippi, 1901:168. Type locality “Provincia de Copiapó,” Chile.

*Canis maullinicus* Philippi, 1903:158. Type locality “Provincia Llanquihue ad occidentem lacus Llanquihue, Loco, Nueva Braunau,” Chile.

*Canis trichodactylus* Philippi, 1903:158. Type locality “Provincia Valdivia,” Chile.

*Canis torquatus* Philippi, 1903:159. Type locality “Puerto Montt,” Llanquihue, Chile.

*Pseudalopex azarica* Thomas, 1914:360. Type locality “Mar del Plata, S. E. Buenos Ayres,” Argentina.

[*Canis* [(*Pseudalopex* )]] *gymnocercus attenuatus* Kraglievich, 1930:54. Type locality “los Estados brasileños de Rio Grande del Sur, Paraná y tal vez Matto Grosso,” Brazil.

*Pseudalopex gymnocercus gymnocercus*: Cabrera, 1931:64. Name combination.

*Dusicyon* (*Dusicyon*) *gymnocercus*: Osgood, 1934:49. Name combination.

*Lycalopex gymnocercus*: Zunino et al., 1995:739. First use of current name combination.



**Fig. 1.**—An adult female *Lycalopex gymnocercus* from E. Tornquist Provincial Park, Buenos Aires Province, Argentina. Used with permission of the photographer O. Fernández.

CONTEXT AND CONTENT. Order Carnivora, family Canidae, subfamily Caninae. Five subspecies were recognized by Wozencraft (2005):

*L. g. antiquus* (Ameghino, 1889:298); see above.

*L. g. domeykoanus* (Philippi, 1901:168); see above.

*L. g. gracilis* (Burmeister, 1861:406); see above.

*L. g. gymnocercus* (Fischer, 1814:178); see above.

*L. g. maullinicus* (Philippi, 1903:158); see above.

Subspecific boundaries and allocation of subspecies synonyms remain uncertain in the absence of a detailed systematic overview assessing geographic variation.

NOMENCLATURE NOTES. The taxonomic status of the Pampas fox and other related species is controversial. Canids of this genus were alternatively included in the genus *Canis* (Langguth 1975), *Dusicyon* (Langguth 1969), and *Pseudalopex* (Thomas 1914). Initially, *Pseudalopex* was used as a subgenus (Kraglievich 1930; Langguth 1969), then later Langguth (1975) and Van Gelder (1978) placed *Pseudalopex* as a subgenus of *Canis*, excluding *Dusicyon australis*. Clutton-Brock et al. (1976) included *australis*, *culpaeus*, *griseus*, *gymnocercus*, and *vetulus* in *Dusicyon*. However, Berta (1988) gave full generic recognition to *Pseudalopex*, arguing that the species within this genus (*culpaeus*, *griseus*, *gymnocercus*, *sechurae*, and *vetulus*) share derived features that indicate a single origin, separated from other extinct genera that are more closely related to *D. australis*. More recently, Zunino et al. (1995) proposed that *P. griseus* and *P. gymnocercus* represent clinal variants of *Lycalopex gymnocercus*. They considered *Lycalopex* as the valid genus name because it was used previously by Burmeister (1854). Chromosome analyses by Gallardo and Formas (1975) and Vitullo and Zuleta (1992) supported this assignment. The most recent revisions of canid phylogeny (Bininda-Emonds et al. 1999; Zrzavý and Řičánková 2004) suggest that all South American fox-like canids (“zorros”) form a single clade and that they should be classified under the same generic name of *Lycalopex*. Accordingly, Wozencraft (2005) assigned all “zorros” (with the exception of the extinct Falkland Island fox [*D. australis*]) to *Lycalopex*.

Only 3 subspecies were recognized by Massoia (1982), who suggested that along the borders of their respective distribution ranges they would interbreed. Two of them (*L. g. antiquus* and *L. g. gymnocercus*) also are listed by Wozencraft’s (2005) most recent taxonomical revision, whereas *L. g. lordi* (Massoia, 1982:149. Type locality “Los Noques, Finca Saladillo, 50 km de la ciudad de Salta, departamento de Gral. M. M. de Güemes, Provincia de Salta, República Argentina”) is only recognized by Massoia (1982).

## DIAGNOSIS

*Lycalopex gymnocercus* is similar in size to *L. culpaeus* but has a proportionally wider rostrum relative to palate

length (27–32% versus 24%) and less reddish coloration of head, neck, and ears than *L. culpaeus* (Clutton-Brock et al. 1976; Novaro 1997). *L. gymnocercus* is larger (mean body mass = 4–6 kg; length of hind foot = 128–145 mm) than *L. griseus* (mean body mass = 2.5–4 kg; length of hind foot = 122–130 mm) but otherwise similarly colored and similarly proportioned. There is less separation between the minimum constriction of frontal bones and the postorbital apophysis in *L. gymnocercus* than in *L. griseus* (Gonzalez del Solar and Rau 2004; Lucherini et al. 2004). The forelegs of *L. gymnocercus* are gray externally and the soles of the feet are blackish brown, whereas the forelegs are entirely red-yellow in *L. griseus* and soles of the feet are red-brown (Gray 1869).

## GENERAL CHARACTERS

*Lycalopex gymnocercus* (Fig. 1) is a medium-sized fox. Its skull is somewhat triangular, with a long facial region and a robust and high interparietal crest. Canines and premolars are “fox-like” (i.e., the carnassials are simple and increase in size at the expense of the molars—Clutton-Brock et al. 1976; Kraglievich 1930). Pelage on the top and sides of the head is reddish and on the dorsal rostrum is reddish to black. The ventral surface of the head is pale gray to white. Ears are triangular, broad, relatively large, and are reddish on the outer surface and white on the inner surface. Back, shoulders, and flanks are gray. A blackish line runs along the center of the back and tail. The tail is relatively long (>50% of the length of head and body), bushy, and gray with a black tip. Belly and inner surface of legs are pale gray to whitish. Hind limbs are gray laterally with distal portions reddish with a characteristic black spot on the lower rear side. Lateral surface of the front limbs is reddish (Clutton-Brock et al. 1976; Crespo 1971; Redford and Eisenberg 1992). Body size varies geographically. Published mean measurements of body mass (kg) and total body length (mm) for adults (range and *n* in parentheses) are: 5.95 (4.5–7.9, 26, in western Uruguay—Barlow 1965), 3.97 (2.4–5.0, 11, in Argentina/Paraguay—Redford and Eisenberg 1992), and 590.9 (520–722, 23, in Argentina/Paraguay—Redford and Eisenberg 1992). Mean measurements (range and *n* in parentheses) of body mass (kg) and total body length (mm) obtained from immobilized adult specimens used in our radiotracking study from December 1998 to February 2005 in southern Buenos Aires Province were 5.41 (2.4–8.0, 54) and 646 (505–800, 34).

Adult males are larger than females in La Pampa Province, central Argentina (mean body mass = 4.63 kg, *n* = 116, versus 4.21 kg, *n* = 163—Crespo 1971), Buenos Aires Province, central Argentina (5.95 kg, *n* = 31, versus 4.67 kg, *n* = 24—obtained from specimens used in our radiotracking study), and Colonia Department, southern Uruguay (5.88 kg, *n* = 11, versus 4.61 kg, *n* = 8—Cravino et al. 2000).

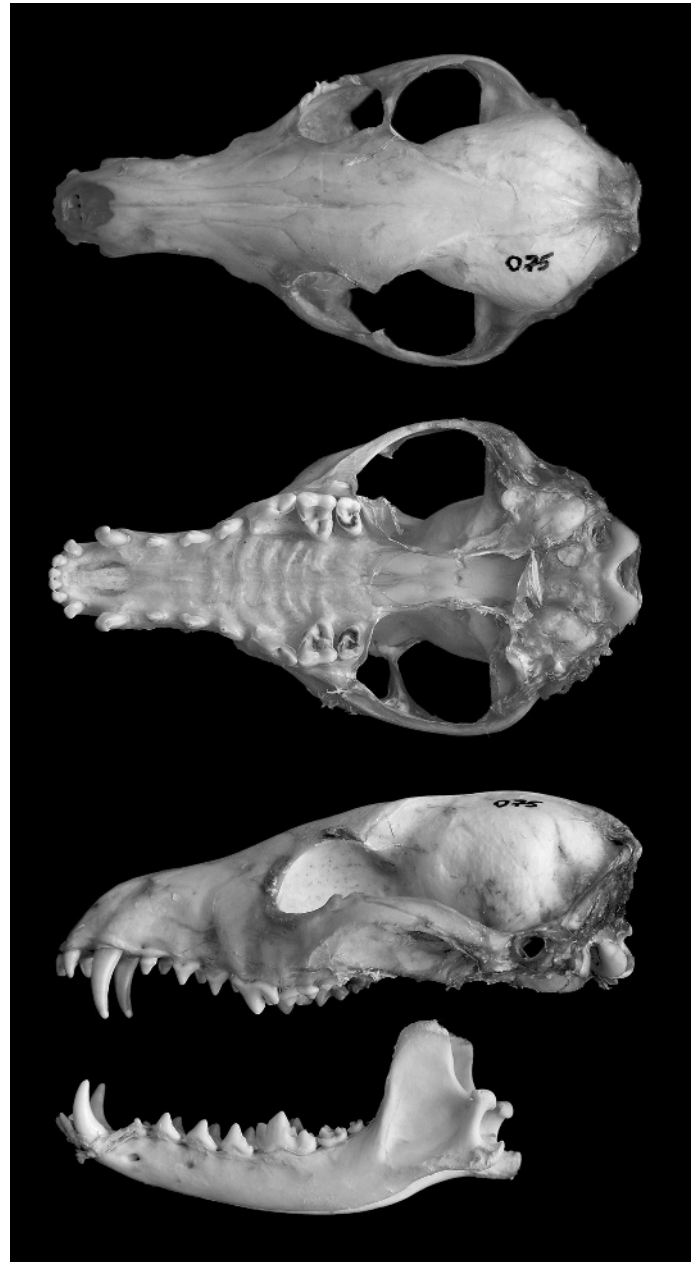
External measurements (mean in mm for males and females, respectively; range and *n* in parentheses) for Pampas foxes from La Pampa Province, Argentina, were: length of head and body, 648 (597–700, 10), 621 (535–683, 16); length of tail, 352 (320–365, 10), 319 (270–356, 16); length of hind foot, 140 (135–155, 10), 128 (115–145, 16); length of ear, 86 (80–90, 10), 84 (80–90, 16—Crespo 1971). We recorded similar data from Pampas foxes from Buenos Aires Province, Argentina; measurements were: length of head and body, 683 (590–800, 26), 650 (590–720, 21); length of tail, 358 (280–430, 31), 333 (265–390, 23); length of hind foot, 147 (130–150, 17), 132 (120–145, 15); length of ear, 72 (66–81, 17), 74 (63–81, 15).

Cranial measurements (means, in mm, with ranges in parentheses) for adult males (*n* = 18) and females (*n* = 19), respectively, were: total length, 143.6 (130–154.3), 134.9 (129.3–143); zygomatic width, 75.7 (69.6–79.0), 71.3 (67.0–76.1); mastoid width, 44.2 (42.5–47.0), 42.3 (39.7–44.3); length of mandible, 106.3 (100.0–111.0), 101.3 (97.4–107.2—Crespo 1971; Fig. 2). Gross morphology of the brain of *L. gymnocercus* is very similar to that of the other *Lycalopex* species. The proreal gyrus is bilaterally constricted and the orbital gyri have 1 sulcus that separates the proreal and orbital gyri (Lyras and Van der Geer 2003).

## DISTRIBUTION

*Lycalopex gymnocercus* occurs in eastern Bolivia, western and central Paraguay, Uruguay, north and central Argentina, and southeastern Brazil (Fig. 3; Crespo 1971; Lucherini et al. 2004; Massoia 1982). In Argentina, it is found from the foothills of the Andes in eastern Salta, Jujuy, Catamarca, San Juan, La Rioja, and Mendoza provinces to the Atlantic coast in Buenos Aires Province, Rio Negro Province, and possibly Chubut Province to the south (Díaz and Lucherini 2006; Lucherini et al. 2004). The Pampas fox prefers open habitats but also occurs in areas of Pampas grassland modified by extensive ranching and agriculture activities (Lucherini et al. 2004). In the driest habitats in the southerly and easterly parts of its range, *L. gymnocercus* is replaced by *L. griseus* (Lucherini et al. 2004). Its present range coincides largely with its historic range.

The geographic limits of the ranges of subspecies are not precise. However, *L. g. gymnocercus* generally occurs in subtropical grasslands of northeastern Argentina (southern Misiones, northern Corrientes, and eastern Formosa provinces), Uruguay, Paraguay, and southeastern Brazil (from Paraná to Rio Grande do Sul). *L. g. antiquus* is 1 of only a few subspecies of mammals with ranges restricted to the zoogeographical Pampean dominion (Ringuelet 1955) in central Argentina (from Córdoba and San Luis provinces to the Río Negro, and from the Atlantic coast to a poorly defined limit west of the Salado-Chadilevú River). The subspecific identity of Pampas foxes occurring in the area that runs through most of northern Argentina, northwestern Paraguay, and southeastern Bolivia is unknown (Fig. 3). The type locality of 3 of the



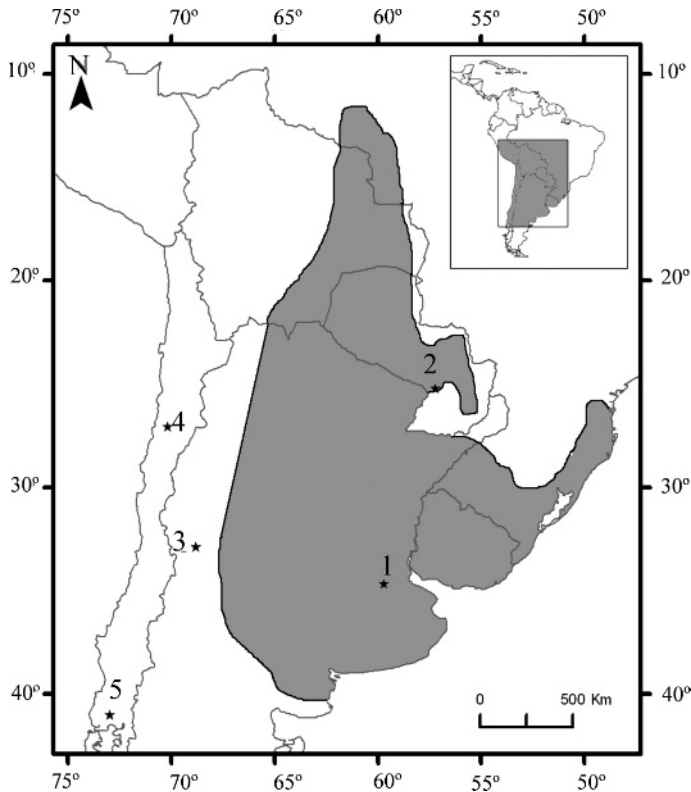
**Fig. 2.**—Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Lycalopex gymnocercus* (GECM [Universidad Nacional del Sur, Departamento de Biología, Bioquímica y Farmacia, Cátedra Fisiología Animal collection] 075) from Tornquist Provincial Park, Buenos Aires Province, Argentina. Occipitonasal length is 141.9 mm.

subspecies described by Wozencraft (2005) falls outside the known present range of *L. gymnocercus* (Fig. 3).

## FOSSIL RECORD

The oldest known fossils of *Lycalopex* have been found in deposits from the Chapadmalalan age (3.0–2.5 million





**Fig. 3.**—Geographic distribution of *Lycalopex gymnocercus*. Stars indicate subspecies type localities: 1, *L. g. antiquus*; 2, *L. g. gymnocercus*; 3, *L. g. gracilis*; 4, *L. g. domeykoanus*; 5, *L. g. maullinicus*. Map redrawn with modifications from Lucherini et al. (2004) with editors' permission.

years ago; Pliocene) in north-central Chile (Moreno et al. 1994). The earliest record of *L. gymnocercus* is from the Vorohué Formation, Buenos Aires Province, Argentina, and is Uquian in age (2.5–1.5 million years ago; late Pliocene and early Pleistocene—Berta 1987; Kraglievich 1952). *L. gymnocercus* is recorded from sediments of the La Chumbiada Member of the Luján Formation in Argentina that are about 30,000 years old (Tonni et al. 1999).

### FORM AND FUNCTION

The fur of *Lycalopex gymnocercus* becomes thicker and longer in winter. Guard hairs have nonoverlapping, lanceolate-romboidal, cuticular scales at the proximal end (Vázquez et al. 2000). Medullary portion of hair has a reticular nonfragmented lattice (Chéhebar and Martín 1989; Vázquez et al. 2000). Locomotion is digitigrade. Front feet have 5 toes, 4 with full claws and 1 with a dew claw; hind feet have 4 toes (Redford and Eisenberg 1992). Tracks can be confused with those of other fox-like canids that have 4 toes with short claws in both front and hind feet, because the digit with the dewclaw does not form a visible track. Toe marks are well-separated ovals. In Buenos Aires Province,

Argentina, track measurements (mean in cm with range and *n* in parentheses) were: maximum length, 3.7 (2.0–4.9, 64); maximum width, 2.9 (1.1–3.8, 63) for front foot; maximum length, 3.5 (1.3–6.2, 66); maximum width, 2.5 (0.7–3.5, 66) for hind foot (data obtained from specimens immobilized for our radiotracking study from December 1998 to February 2005).

Mass and dimensions of testicles vary seasonally, reaching maximums in August. Mean mass of the paired testicles varied from 1 g to 16 g (*n* = 80—Crespo 1971). Length and width of testicles (mean in mm with range in parentheses, for 13 male specimens used in our radiotracking study) were: 2.8 (1.2–4.6), 2.4 (1.7–3.7).

The dental formula for *L. gymnocercus* is  $i\ 3/3, c\ 1/1, p\ 4/4, m\ 2/3$ , total 42 (Redford and Eisenberg 1992). Dental morphology, in particular the large grinding areas of the molars compared to other canids, shows that *L. gymnocercus* is adapted to an omnivorous diet (Márquez and Fariña 2003).

Feces were variable in dimensions in Tornquist Park, southern Buenos Aires Province; measurements (mean  $\pm$  SE measurements, *n* in parentheses) were: length,  $99.8 \pm 4.4$  mm (135); maximum diameter,  $15.70 \pm 0.31$  mm (115); dry mass,  $5.61 \pm 0.44$  g (162—Castillo 2002); in Campos del Tuyú Reserve, northern Buenos Aires Province: length,  $118 \pm 31$  mm (34); maximum diameter,  $16 \pm 4$  mm (38—Vuillermoz and Sapoznikow 1998).

### ONTOGENY AND REPRODUCTION

Gestation lasts 55–60 days. Mean number of embryos per female is 3.4 (*n* = 72 females) and litter size ranges from 1 to 8 (mean, 3.35—Crespo 1971). The frequency of in utero reabsorption of embryos ranges from 40% to 100% (*n* = 4 females). Females are monestrous and an average of 85% of adult females in a given season are impregnated (Crespo 1971). Young are born in spring, from September–October to December. Lactation lasts about 2 months, and females can breed by 8–12 months (Crespo 1971; Redford and Eisenberg 1992).

### ECOLOGY

**Population characteristics.**—*Lycalopex gymnocercus* is considered either abundant or common in most areas (Lucherini et al. 2004). Reported densities of Pampas foxes were: 1.04 foxes/km<sup>2</sup> (La Pampas, Argentina—Crespo 1971), 1.8 foxes/km<sup>2</sup> (Bañados del Izozog, Bolivian Chaco—Ayala and Noss 2000), and 0.64 fox “groups”/km<sup>2</sup> (Paraguayan Chaco—Brooks 1992). In the Paraguayan Chaco, abundance may be correlated with annual rodent abundance (Brooks 1992). Based on these estimated densities, rough total counts of >150,000, 180,000, and 350,000 individuals were obtained for La Pampa Province, Paraguayan Chaco,

and Bolivian Chaco, respectively (Lucherini et al. 2004). In Buenos Aires Province, Argentina, a population density of 0.62–5.85 foxes/km<sup>2</sup> in the densest areas and 0.47–2.94 foxes/km<sup>2</sup> in a less-dense area was estimated (Luengos Vidal 2003). In the same region, populations decreased from 1998 to 2002, possibly due to increased hunting pressure (Luengos Vidal 2003). However, in La Pampa Province, examination of data from scent stations indicated that abundance was stable between 1992 and 1998 (R. Dosio and M. Pessino, in litt.). In northern Patagonia, signs of presence and visitation rates of *L. gymnocercus* at scent-stations suggested that its population was larger than those of the Molina's hog-nosed skunk (*Conepatus chinga*), lesser grison (*Galictis cuja*), and white-eared opossum (*Didelphis albiventris*—García and Kittlein 2005). Similarly, trapping rates and frequency of observation suggested that the population size of Pampas foxes was greater than that of skunk, lesser grison, and Geoffroy's cat (*Leopardus geoffroyi*) in southern Pampas (Luengos Vidal et al. 2005).

Sex ratios favor males. In Buenos Aires Province, a population of *L. gymnocercus* consisting of 60.3% adults, 31.3% juveniles, and 6.3% pups had a 1.4:1 male:female ratio ( $n = 63$ —Luengos Vidal 2003). In La Pampa Province, the male:female ratio was 1.03:1 ( $n = 324$ ) in a population with 52.8% adults, 34.3% juveniles, and 12.9% pups (Crespo 1971).

Maximum longevity of *L. gymnocercus* in captivity is nearly 14 years (Jones 1982), but few individuals are likely to live more than a few years in the wild (Crespo 1971; Lucherini et al. 2004). Annual survival in the wild was reported as 7% for adults and 21.8% for juveniles (Crespo 1971).

**Space use.**—*Lycalopex gymnocercus* prefers open areas, tall grass plains, and subhumid to dry habitats, but occurs in puna, open grasslands, Andean tropical forest, semideciduous lower montane forest, Argentine Monte, Chaco forest, dry scrubland, open thorn woodland, marshes, wetlands, coastal sand dunes, Pampas grassland, overgrazed pastures, and cropland areas of the Pampas (Brooks 1992; Díaz and Lucherini 2006; García and Kittlein 2005; Lucherini et al. 2004; Redford and Eisenberg 1992). *L. gymnocercus* is generally found at elevations <1,000 m but can reach 3,500 m in the puna highlands (Jayat et al. 1999). When sympatric with crab-eating foxes (*Cerdocyon thous*), *L. gymnocercus* is more abundant in open habitats, whereas *C. thous* is more abundant in woodland areas (Vieira and Port 2007).

**Diets.**—Pampas foxes are generalist and adaptable predators. Diet varies geographically, even at a relatively small scale (Farias and Kittlein 2008), and includes both domestic and wild vertebrates, particularly European hares (*Lepus europaeus*), rodents (mainly of the genera *Akodon*, *Calomys*, *Cavia*, *Ctenomys*, *Eligmodontia*, *Graomys*, *Microcavia*, *Oligoryzomys*, *Phyllotis*, and *Reithrodon*), and birds (tinamous of the family Tinamidae, and also Passeriformes and Columbiformes), as well as fruit (both autochthonous

[*Acacia aroma*, *Celtis tala*, *Condalia microphylla*, and *Prosopis caldenia*] and introduced [*Prunus mahleb* and *Rosa*]), insects (especially Coleoptera, Diptera, Hymenoptera, Homoptera, Odonata, Orthoptera, and larvae of Lepidoptera and Coleoptera), carrion, and garbage. Additional prey includes opossums (*D. albiventris*), armadillos (*Chaetophractus villosus*, *C. vellerosus*, *Dasyus hybridus*, and *Zaedyus pichiy*), lizards, fish, snails, crabs, and scorpions (Castillo 2002; Cravino et al. 2000; Crespo 1971; Farias 2000; Farias and Kittlein 2008; García and Kittlein 2005; Luengos Vidal et al. 2003a; Pradella Dotto 1997; Vieira and Port 2007; Vuillermoz and Sapoznikow 1998). In La Pampa Province, Argentina, introduced European hares, plains viscachas (*Lagostomus maximus*), and other smaller rodents were the most important food items, followed by birds and carrion (Crespo 1971). In Buenos Aires Province, Argentina, food items included high frequencies of rodents, European hares, birds, insects, and fruits (Castillo 2002; Farias 2000; Farias and Kittlein 2008; García and Kittlein 2005; Luengos Vidal et al. 2003a).

In the Pampas mountain grasslands of Buenos Aires Province, Argentina, the frequency of occurrence of vertebrate and invertebrate prey in fecal samples were similar (75.1% and 71.1%, respectively—Castillo 2002). At Laguna Mar Chiquita, Buenos Aires Province, invertebrates comprised 53.9% of all food items, but mammal carrion, rodents, and European hares dominated the ingested biomass (Farias 2000; Farias and Kittlein 2008). Similarly, in a coastal area of northern Patagonia, Argentina, European hares and rodents contributed most to ingested biomass in summer, in spite of the greater frequency of occurrence of insects and fruits (García and Kittlein 2005). The importance of introduced hares in diets of *L. gymnocercus* illustrates its capacity to exploit new, abundant prey. In La Pampa Province, Argentina (Crespo 1971), and Colonia Department, Uruguay (Cravino et al. 2000), wild mammals (especially small rodents) were the most frequent food. Domestic mammals contribute up to 48.6% of all prey items (Pradella Dotto 1997) in Rio Grande do Sul, Brazil, and 17.9% in Colonia Department, Uruguay (Cravino et al. 2000), but they are rare in other areas (Farias 2000; García and Kittlein 2005). Apparently, adult sheep (*Ovis aries*) are mainly scavenged (Lucherini et al. 2004), but there is some evidence of predation on newborn lambs. This predation was only a secondary factor in lamb mortality (2.9% of total lamb mortality in Uruguay [Cravino et al. 1997] and 4.1% and 6.9% in Rio Negro Province, Argentina [Bellati 1980; Olachea et al. 1981, respectively]). Although Pampas foxes are commonly accused of reducing poultry and game populations, particularly by preying on chicks and eggs of ground-nesting birds, there are few data to support this assertion (Farias 2000; Vuillermoz and Sapoznikow 1998).

In a Pampas mountain grassland, fruit (mainly of introduced *P. mahleb* and *Rosa canina*) are more frequently

consumed in spring, Coleoptera in spring and summer, and Orthoptera in summer and autumn, whereas rodents were the most important food in winter (Castillo 2002). Diet also varies among habitats within the same area (García and Kittlein 2005) and locally (Farias and Kittlein 2008); variations have been attributed to fluctuations in food availability (Castillo 2002; Farias 2000; Farias and Kittlein 2008; García 2001; Luengos Vidal et al. 2003a; Vuillermoz and Sapoznikow 1998). *L. gymnocercus* may contribute to the dispersion of fruit seeds (especially *A. aroma* and *C. tala*) in the Chaco ecoregion (Varela and Bucher 2006). We occasionally observed food remains at den sites, suggesting that young feed mostly on small to medium-sized vertebrate prey.

Studies of diet overlap indicate that *L. gymnocercus* probably competes for food with the similar-sized crab-eating fox, Geoffroy's cat, and possibly Pampas cat (*Leopardus pajeros*—Lucherini et al. 2004). In Uruguay and Brazil, extensive overlap in trophic niche occurs between sympatric Pampas foxes and crab-eating foxes (Cravino et al. 2000; Vieira and Port 2007, respectively). However, the diet of *C. thous* (e.g., Facure et al. 2003, Jácomo et al. 2004) is more frugivorous than that of *L. gymnocercus* (García and Kittlein 2005), as would be expected given their dental morphology (Márquez and Fariña 2003). In Buenos Aires Province, most of the prey items of *L. gymnocercus* and Geoffroy's cat were the same (e.g., *Cavia*, *Oligoryzomys*, and *Akodon* rodents; European hares; and small passerines and doves), although their frequency of occurrence was different and vertebrate prey was a more important food for Geoffroy's cats than for Pampas foxes (Luengos Vidal et al. 2003a; Manfredi et al. 2004; Vuillermoz and Sapoznikow 1998). Partial food niche overlap between Pampas foxes and lesser grisons in Buenos Aires Province also has been observed in our study area.

In Lihuel Calel National Park, in central Argentina, remains of armadillos (*Z. pichiy* and *C. villosus*), plain viscachas, small rodents (*Ctenomys* and *Galea musteloides*), and European hares were found in the feces of both pumas (*Puma concolor*) and Pampas foxes (M. Pessino, in litt.). However, it is likely that pumas, because of their considerably larger body size, are more important as predators than as competitors of Pampas foxes.

**Diseases and parasites.**—A variety of parasites have been reported for *L. gymnocercus*. Ectoparasites include ticks (*Amblyomma maculatum* and *A. auriculare*) and fleas (*Ctenocephalides felix*, *Hectopsylla broscus*, *Malacopsylla grossiventris*, *Polygenis*, *Pulex irritans*, and *Tiamastus cavicola*—Lucherini et al. 2004). Cases of *Sarcoptes scabiei* infection have been reported (S. Deem, pers. comm.). Endoparasites include *Dipylidium caninum* (Dilepididae), *Joyeuxiella* (Dilepididae), *Taenia pisiformis* (Taenidae), and other species of Cestoda. Nematodes such as *Ancylostoma caninum* (Ancylostomidae), *Molineus felineus* (Trichostrongylidae), *Toxocara canis* (Ascariidae), *Ancylostoma caninum*

(Ancylostomidae), *Rictularia* (Rictularidae), and *Physaloptera* (Physalopteridae—Led et al. 1970), as well as *Echinococcus granulosus* and *E. cepanzyi*, also have been noted. Another internal parasite, *Athesmia foxi* (Trematoda: Dicrocoeliidae), was found in the small intestine (Lucherini et al. 2004). Captive Pampas foxes are susceptible to parvovirus and canine distemper (Lucherini et al. 2004).

**Interspecific interactions.**—Predators of *L. gymnocercus* include puma (M. Pessino, in litt.) and feral dogs (Lucherini et al. 2004). They are also frequently struck by cars. However, hunting is likely a primary cause of mortality of *L. gymnocercus*. In the Argentinean provinces of La Pampa, Buenos Aires, and San Luis, legal control campaigns were carried out between 1949 and the early 1970s, to reduce economic losses caused by *L. gymnocercus* predation upon sheep and goats; 361,560 Pampas foxes were killed by a variety of methods (e.g., leghold traps, selective traps with toxic cartridges, shooting, dogs, and poisoned baits—Godoy 1963, M. Pessino and R. Sosa, in litt.).

**Miscellaneous.**—In some areas Pampas fox fat is used for medicinal purposes (Lucherini et al. 2004). *L. gymnocercus* has been traditionally hunted for its fur in Argentina and Uruguay (Lucherini et al. 2004). From 1975 to 1985, *Lycalopex* skins (mostly belonging to *L. gymnocercus*—García Fernández 1991) were among the most numerous to be exported legally from Argentina (Chebez 1994). However, exports declined later, mainly due to a decrease in demand (Novaro and Funes 1994), to 8,000 specimens per year from 1997 to 1999 (M. Elisetoh, pers. comm.).

In Argentina, *L. gymnocercus* has been successfully bred in captivity and presently is the best represented carnivore species in captivity in the country (Aprile 1999).

In an evaluation of 3 restraining devices for capturing Pampas foxes, Luengos Vidal et al. (2003b) found that box-traps were least effective, whereas neck snares and foothold traps were equally more effective. There was no significant difference in the average levels of damage caused by the 3 devices. Neck snares were the most selective trapping devices, avoiding the capture of nontarget carnivores. An average of 69.9 trap days were necessary to trap a Pampas fox. Trapping efficiency varied seasonally and peaked in winter (Luengos Vidal et al. 2003b).

## BEHAVIOR

In Paraguay and Brazil, *Lycalopex gymnocercus* was reported to be active throughout the 24-h period (Brooks 1992; Vieira and Port 2007, respectively). However, in Buenos Aires Province, central Argentina, *L. gymnocercus*, which spent most of its time resting (67%, range 58.9–84.9%, of 5,168 activity fixes from 7 radiocollared individuals), was more active at night (45.8%) than at dusk and dawn (35.6% and 26.1%, respectively) or during the day (24%—Araujo



2004). Peak activity seasons were summer and autumn (November–April—Araujo 2004).

Pampas foxes typically forage solitarily. They have been observed to cache food when it is abundant (García and Kittlein 2005). Dens can be located in a variety of shelters, such as natural rocky caves, holes in tree trunks, and burrows of other animals (e.g., armadillos and plains viscachas—Lucherini et al. 2004). At our field site we observed that Pampas foxes usually sought shelter amidst tall vegetation in the Pampas grasslands and young were frequently moved to new dens. We also recorded that young remain in dens until at least the age of 3 months. Both mates have been observed to guard the den and males provide food to pups and females at den. In a Sierra Pampas area, we noticed that reproductive dens did not appear to be reused in following years.

*Lycalopex gymnocercus* may form monogamous pairs. Pairs are frequently observed from mating until pups leave the natal den (Lucherini et al. 2004). However, they hunt and spend most of their time alone: in the Paraguayan Chaco (Brooks 1992) and La Pampa Province, Argentina (Branch 1994), 88% and 93% of observations, respectively, were of single individuals.

The long-distance calls of Pampas foxes peak in frequency during the breeding period and may serve to maintain contact between pair members, as well as to advertise territories (Branch 1994). During the breeding season, we observed both pair mates using a brief and repeated alarm call when detecting potential threats to the young.

The use of latrines and defecation site features suggest that scats are used in intraspecific communication (García and Kittlein 2005). In Buenos Aires Province, central Argentina, Pampas foxes showed a relatively low frequency of reuse of scat marking sites, and a tendency to defecate in latrines used by *L. geoffroyi* and *C. chinga* (Manfredi 2007). In the same area, through a radiotracking study from December 1998 to February 2005, we calculated the average home range of 8 adult Pampas foxes as 263.4 ha (range, 55–461 ha).

## CONSERVATION

*Lycalopex gymnocercus* has been assigned to the “Least Concern” category by the Argentina Red List of Mammals (Díaz and Ojeda 2000) and the International Union for the Conservation of Nature and Natural Resources Canid Specialist Group (Lucherini et al. 2004). It is also listed in the Appendix II of Convention on International Trade in Endangered Species of Wild Fauna and Flora (Medel and Jacksic 1988). In Brazil, in spite of the fact that *L. gymnocercus* is protected by law, control measures are regularly taken by sheep breeders with no legal permission (C. Indrusiak, in litt.) and, in Uruguay, the government

grants special hunting authorization to control predation on sheep herds (Cravino et al. 2000). The international trade of *L. gymnocercus* has been banned by its inclusion in Appendix II of CITES (Medel and Jacksic 1988). However, the sum of widespread illegal hunting by rural people, which caused population decreases in the Argentina provinces of Tucumán (Bárquez et al. 1991) and Salta (Cajal 1986), the implementation by official organizations of control measures with the use of bounty systems, and the massive alteration of natural habitats in most of the range of the species represent actual threats for the populations of *L. gymnocercus* (Lucherini et al. 2004).

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## LITERATURE CITED

- AMEGHINO, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Acta Academia Nacional de Ciencias de la República Argentina en Córdoba 6:1–1027.
- APRILE, G. 1999. Registro de animales silvestres autóctonos en establecimientos zoológicos de la República Argentina. Fundación Vida Silvestre Argentina, Buenos Aires, Argentina.
- ARAUJO, M. S. 2004. Estudio radiotelemétrico del patrón de actividad del zorro gris pampeano *Pseudalopex gymnocercus* en el Parque Provincial E. Tornquist. Licenciatura thesis, Universidad Nacional del Sur, Bahía Blanca, Argentina.
- AYALA, J., AND A. NOSS. 2000. Censo por transectas en el Chaco Boliviano: limitaciones biológicas y sociales de la metodología. Pp. 29 in Manejo de fauna silvestre en Amazonia y Latinoamérica (E. Cabrera, C. Mercolli, and R. Resquin, eds.). Ricor Grafic S.A., Asunción, Paraguay.
- AZARA, F. 1801. Essais sur l'histoire naturelle des quadrupèdes de la province du Paraguay. Traduits sur le manuscrit inédit de l'auteur. Pra. M. L. E. Modeau-Saint-Méry. Charles Pougens, Paris, France.
- BARLOW, J. C. 1965. Land mammals from Uruguay. Ecology and zoogeography. Ph.D. dissertation, University of Kansas, Lawrence.
- BÁRQUEZ, R., M. MARES, AND R. OJEDA. 1991. Mamíferos de Tucumán. Oklahoma Museum of Natural History, University of Oklahoma Foundation, Inc., Norman.
- BELLATI, J. 1980. Datos preliminares de predación perinatal ovina en el oeste de la Provincia de Río Negro. INTA (Instituto Nacional de Tecnología Agropecuaria) Estación Experimental Producción Animal. Bariloche, Memórias Técnicas 4:80–89.
- BERTA, A. 1987. Origin, diversification, and zoogeography of the South American Canidae. Fieldiana: Zoology 39:455–471.

- BERTA, A. 1988. Quaternary evolution and biogeography of the large South American Canidae (Mammalia, Carnivora). University of California Publications, Geological Sciences 132:1–149.
- BININDA-EMONDS, O. R. P., J. L. GITTLEMAN, AND A. PURVIS. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews of the Cambridge Philosophical Society* 74: 143–175.
- BRANCH, L. C. 1994. Seasonal patterns in long-distance vocalizations of the Pampas fox. *Vida Silvestre Neotropical* 3:108–111.
- BROOKS, D. 1992. Notes on group size, density, and habitat association of the Pampas fox (*Dusicyon gymnocercus*) in the Paraguayan Chaco. *Mammalia* 56:314–316.
- BURMEISTER, H. 1854. *Sistematische Übersicht der Thiere Brasiliens, Welche während einer Reise durch die Provinzen von Rio de Janeiro und Minas Geraës gesammelt oder beobachtet wurden von Dr. H. Burmesiter. Säugethiere (Mammalia)*. Georg Reimer, Berlin, Germany.
- BURMEISTER, H. 1861. *Reise durch die La Plata Staaten, mit besonderer Rücksicht auf die Physische Beschaffenheit und die Culturzustand der Argentinische Republik. Ausgeführt in den Jahren 1857, 1858, 1859 und 1860. Vol. 2 (Die nordwestlichen Provinzen und die Cordilleren zwischen Catamarca und Copiapó umfassend)*. H. W. Schmidt, Halle, Germany.
- CABRERA, A. 1931. On some South American canine genera. *Journal of Mammalogy* 12:54–67.
- CABRERA, A. 1958. Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”*, Ciencias Zoológicas 4:1–308.
- CAJAL, J. L. 1986. *El recurso fauna en Argentina. Antecedentes y cuadro de situación actual*. Ministerio de Educación y Justicia, Secretaría de Ciencia y Técnica, Buenos Aires, Argentina.
- CASTILLO, D. F. 2002. Composición y variación estacional de la dieta del zorro pampeano (*Pseudalopex gymnocercus*) en el Parque Provincial Ernesto Tornquist. *Licenciatura thesis, Universidad Nacional del Sur, Bahía Blanca, Argentina*.
- CHEBEZ, J. C. 1994. Los que se van. *Especies argentinas en peligro*. Albatros, Buenos Aires, Argentina.
- CHÉHEBAR, C., AND S. MARTÍN. 1989. Guía para el reconocimiento microscópico de los pelos de los mamíferos de la Patagonia. *Doñana, Acta Vertebrata* 16:247–291.
- CLUTTON-BROCK, J., G. B. CORBET, AND M. MILLS. 1976. A review of the family Canidae, with a classification by numerical methods. *Bulletin of the British Museum (Natural History), Zoology* 29: 117–199.
- CRAVINO, J. L., M. E. CALVAR, M. A. BERRUTI, N. A. FONTANA, AND J. C. POETTI. 1997. American Southern Cone foxes: predators or prey? An Uruguayan study case. *Journal of Wildlife Research* 2: 107–114.
- CRAVINO, J. L., ET AL. 2000. Análisis holístico de la predación en corderos. Un estudio de caso, con énfasis en la acción de “zorros” (Mammalia, Canidae). Premio Nacional de la Academia de Medicina de Veterinaria del Uruguay, Montevideo, Uruguay.
- CRESPO, J. A. 1971. Ecología del zorro gris *Dusicyon gymnocercus antiquus* (Ameghino) en la provincia de La Pampa. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” e Instituto Nacional de Investigación de las Ciencias Naturales, Ecología* 5:147–205.
- DÍAZ, G. B., AND R. A. OJEDA. 2000. Libro rojo de los mamíferos amenazados de la Argentina. Sociedad Argentina para el Estudio de los Mamíferos, Mendoza, Argentina.
- DÍAZ, M. M., AND M. LUCHERINI. 2006. Mustelidae y Canidae. Pp. 89–93 in *Mamíferos de Argentina: sistemática y distribución* (R. M. Báñez, M. M. Díaz, and R. A. Ojeda, eds.). Sociedad Argentina para el Estudio de los Mamíferos, Mendoza, Argentina.
- FACURE, K. G., A. A. GIARETTA, AND E. L. A. MONTEIRO-FILHO. 2003. Food habits of the crab-eating fox *Cerdocyon thous* in an altitudinal forest of the Mantiqueira Range, southeastern Brazil. *Mammalia* 67:503–511.
- FARIAS, A. A. 2000. Composición y variación estacional de la dieta del zorro gris pampeano (*Pseudalopex gymnocercus*) en la laguna Mar Chiquita (Provincia de Buenos Aires, Argentina). *Licenciatura thesis, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina*.
- FARIAS, A. A., AND M. J. KITTLEIN. 2008. Small-scale spatial variability in the diet of pampas foxes (*Pseudalopex gymnocercus*) and human-induced changes in prey base. *Ecological Research* 23: 543–550.
- FISCHER, G. 1814. *Zoognosia tabulis synopticis illustrata. Volumen Tertium. Nicolas Sergeidis Vsevolozsky. Mosquae. XXIV:1–732*.
- GALLARDO, M., AND F. FORMAS. 1975. The karyotype of *Dusicyon gymnocercus* (Carnivora, Canidae). *Experientia* 31:639–640.
- GARCÍA, V. B. 2001. *Dieta, uso de ambiente y abundancia relativa del zorro gris pampeano, Pseudalopex gymnocercus, en la Reserva de Uso Múltiple Bahía San Blas e Isla Gama, Provincia de Buenos Aires*. Licenciatura thesis, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina.
- GARCÍA, V. B., AND M. J. KITTLEIN. 2005. Diet, habitat use, and relative abundance of pampas fox (*Pseudalopex gymnocercus*) in northern Patagonia, Argentina. *Mammalian Biology* 71:218–226.
- GARCÍA FERNÁNDEZ, J. 1991. Administrando para conservar: el caso de los zorros autóctonos de la Argentina. Pp. 25–36 in *Actas tercera reunión Patagónica sobre el manejo de poblaciones de zorros* (M. C. Funes and A. J. Novaro, eds.). Imprenta Universitaria, Neuquén, Argentina.
- GODOY, J. 1963. *Fauna silvestre. Serie evaluación de los recursos naturales de la Argentina. Tomo VIII, Vols. 1–2. Consejo Federal de Inversiones, Buenos Aires, Argentina*.
- GONZALEZ DEL SOLAR, R., AND J. R. RAU. 2004. Chilla (*Pseudalopex griseus*). Pp. 56–63 in *Canids: foxes, wolves, jackals, and dogs. Status survey and conservation action plan* (C. Sillero-Zubiri, M. Hoffman, and D. W. Macdonald, eds.). International Union for Conservation of Nature and Natural Resources/Species Survival Commission Canid Specialist Group, Gland, Switzerland.
- GRAY, J. E. 1869. Notes on the skulls of the species of dogs, wolves and foxes (Canidae) in the collection of the British Museum. *Proceedings of the Zoological Society of London* 1869:492–525.
- JÁCOMO, A. T. A., L. SILVEIRA, AND J. A. F. DINIZ-FILHO. 2004. Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. *Journal of Zoology (London)* 262: 99–106.
- JAYAT, J. P., R. M. BARQUEZ, M. M. DÍAZ, AND P. J. MARTÍNEZ. 1999. Aportes al conocimiento de la distribución de los carnívoros del Noroeste de Argentina. *Mastozoología Neotropical* 6:15–30.
- JONES, M. L. 1982. Longevity of captive mammals. *Zoologische Garten* 52:113–128.
- KRAGLIEVICH, J. L. 1930. Craneometría y clasificación de los cánidos sudamericanos, especialmente los argentinos actuales y fósiles. *Physis* 10:35–73.
- KRAGLIEVICH, J. L. 1952. Un cánido del Eocuatario de Mar del Plata y sus relaciones con otras formas brasílicas y norteamericana. *Revista del Museo Municipal de Ciencias Naturales y Tradicionales de Mar del Plata, Buenos Aires, Argentina* 1:53–70.
- LANGGUTH, A. 1969. Die südamerikanischen Canidae unter besonderer Berücksichtigung des Mohnenwolfes, *Chrysocyon brachyurus* Illiger. *Zeitschrift für Wissenschaftliche Zoologie* 179:1–188.
- LANGGUTH, A. 1975. Ecology and evolution in the South American canids. Pp. 192–206 in *The wild canids: their systematics, behavioral ecology, and evolution* (M. W. Fox, ed.). Van Nostrand Reinhold Company, New York.
- LED, J. E., J. J. BOERO, AND R. E. FELDMAN. 1970. Pp. 83–89 in *Resúmenes de las V Jornadas Internacionales Facultad de Ciencias Veterinarias, La Plata, Argentina. Los parásitos del zorro “Dusicyon gymnocercus antiquus.”* V Jornadas Internacionales Facultad de Ciencias Veterinarias, La Plata, Argentina.
- LUCHERINI, M., M. PESSINO, AND A. A. FARIAS. 2004. Pampas fox. Pp. 63–68 in *Canids: foxes, wolves, jackals, and dogs. Status survey and conservation action plan* (C. Sillero-Zubiri, M. Hoffman, and D. W. Macdonald, eds.). International Union for Conservation of Nature and Natural Resources/Species Survival Commission Canid Specialist Group, Gland, Switzerland.
- LUENGOS VIDAL, E. M. 2003. Estudio comparado de metodologías de captura y de estimación de las poblaciones de zorro pampeano



- Pseudalopex gymnocercus*. M.S. thesis, Universidad Nacional del Sur, Bahía Blanca, Argentina.
- LUENGOS VIDAL, E. M., D. BIROCHIO, C. MANFREDI, M. LUCHERINI, AND E. B. CASANAVE. 2003a. Ecología trófica y actividad del zorro pampa y del gato montés en el Parque Provincial E. Tornquist. Pp. 127–138 in *Actas II Jornadas Interdisciplinarias del Sudoeste Bonaerense* (M. Vaquero, ed.). EdiUNS, Bahía Blanca, Argentina.
- LUENGOS VIDAL, E. M., LUCHERINI, M., AND CASANAVE, E. B. 2003b. An evaluation of three live-traps for capturing Pampas foxes. *Canid News* 6:1–10.
- LUENGOS VIDAL, E. M., C. MANFREDI, D. CASTILLO, M. LUCHERINI, AND E. B. CASANAVE. 2005. Variaciones en la composición del gremio de carnívoros en la región pampeana. Pp. 97–106 in *Producción, recursos y medioambiente en el Sudoeste Bonaerense—Actas III Jornadas Interdisciplinarias del Sudoeste Bonaerense* (M. Vaquero and M. Cernadas de Bulnes, eds.). EdiUNS, Bahía Blanca, Argentina.
- LUND, P. W. 1840. Fortsaetteise af Pattedyrene. Kaongelige Danske. Videnskaberne Seiskabs Naturvidenskabelige og Mathematisk Afhandlinger, Copenhagen, Denmark.
- LYRAS, G. A., AND A. A. E. VAN DER GEER. 2003. External brain anatomy in relation to the phylogeny of Caninae (Carnivora: Canidae). *Zoological Journal of the Linnean Society* 138:505–522.
- MANFREDI, C. 2007. Nicho trófico y espacial de *Oncifelis geoffroyi* en dos áreas de pastizal pampeano. Ph.D. dissertation, Universidad Nacional del Sur, Bahía Blanca, Argentina.
- MANFREDI, C., M. LUCHERINI, A. CANEPUCCIA, AND E. B. CASANAVE. 2004. Geographical variations in the diet composition of the Geoffroy's cat (*Oncifelis geoffroyi*) in the Pampas grassland of Argentina. *Journal of Mammalogy* 85:1111–1115.
- MÁRQUEZ, A., AND R. A. FARIÑA. 2003. Dental morphology and diet in canids and procyonids from Uruguay. *Mammalia* 67:567–573.
- MASSOIA, E. 1982. *Dusicyon gymnocercus lordi*. Una nueva subespecie del "zorro gris grande" (Mammalia Carnívora Canidae). *Neotropica* 28:147–152.
- MEDEL, R., AND F. M. JACKSIC. 1988. Ecología de los cánidos sudamericanos: una revisión. *Revista Chilena de Historia Natural* 61:67–69.
- MORENO, P. I., C. VILLAGRAN, P. A. MARQUET, AND L. G. MARSHALL. 1994. Quaternary paleobiogeography of northern and central Chile. *Revista Chilena de Historia Natural* 61:159–161.
- NOVARO, A. J. 1997. *Pseudalopex culpaeus*. *Mammalian Species* 558:1–8.
- NOVARO, A. J., AND M. C. FUNES. 1994. Impact of hunting on Argentinean foxes. *Canid News* 2:19–20.
- OLACHEA, F. V., J. P. BELLATI, M. C. SUÁREZ, J. M. PUEYO, AND C. A. ROBLES. 1981. Mortalidad perinatal de corderos en el oeste de la Provincia de Río Negro. *Revista de Medicina Veterinaria* 62:128–134.
- OSGOOD, W. H. 1934. The genera and subgenera of South American canids. *Journal of Mammalogy*, 15:45–50.
- PHILIPPI, R. A. 1866. Ueber ein paar neue Chilenische Säugthiere. *Archiv Für Naturgeschichte* 32:113–117.
- PHILIPPI, R. A. 1901. Nueva especie chilena de zorras. *Anales de la Universidad de Chile* 108:167–170.
- PHILIPPI, R. A. 1903. Einige neue Chilenische Canis-Arten. *Archiv für Naturgeschichte* 69:155–160.
- PRADILLA DOTTO, J. 1997. Estudo da dieta de *Pseudalopex gymnocercus* (Fischer, 1814) e de *Cerdocyon thous* (Linnaeus, 1766) (Mammalia, Canidae) e sua relação com a mortalidade de cordeiros no Rio Grande do Sul. M.S. thesis, Universidade Católica do Rio Grande do Sul, Porto Alegre, Brasil.
- REDFORD, K. H., AND J. F. EISENBERG. 1992. *Mammals of the Neotropics, the Southern Cone*. University of Chicago Press, Chicago, Illinois.
- RINGUELET, R. 1955. Panorama zoogeográfico de la provincia de Buenos Aires. *Notas Museo de La Plata (Zoología)* 18:1–15.
- SCHINZ, H. R. 1821. Das Thierreich nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier. Erster Band. Säugerthiere and Vögel. J. G. Cotta'schen Buchhandlung, Stuttgart and Tübingen, Germany.
- THOMAS, O. 1914. On various South-American mammals. *Annals and Magazine of Natural History, Series 8*. 13:345–363.
- TONNI, E. P., A. L. CIONE, AND A. L. FIGINI. 1999. Predominance of arid climates indicated by mammals in the pampas of Argentina during the late Pleistocene and Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 147:257–281.
- VAN GELDER, R. G. 1978. A review of canid classification. *American Museum Novitates* 2646:1–10.
- VARELA, O., AND E. H. BUCHER. 2006. Passage time, viability, and germination of seeds ingested by foxes. *Journal of Arid Environments* 67:566–578.
- VÁZQUEZ, D. E., P. G. PEROVIC, AND A. A. DE OLSEN. 2000. Patrones cuticulares y medulares de pelos de mamíferos del noroeste argentino (Carnívora y Artiodactyla). *Mastozoología Neotropical* 7:131–147.
- VIEIRA, E. M., AND D. PORT. 2007. Niche overlap and resource partitioning between two sympatric fox species in southern Brazil. *Journal of Zoology (London)* 272:57–63.
- VITULLO, A. D., AND G. A. ZULETA. 1992. Cytogenetics and fossil record: confluent evidence for speciation without chromosomal change in South American canids. *Zeitschrift für Säugetierkunde* 57:248–250.
- VUILLERMOZ, P., AND A. SAPOZNIKOW. 1998. Hábitos alimenticios y selección de presas de los carnívoros medianos en la Reserva de Vida Silvestre "Campos del Tuyú. Fundación Boletín Técnico No. 44. Vida Silvestre Argentina, Buenos Aires, Argentina.
- WOZENCRAFT, W. C. 2005. Order Carnívora. 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.
- ZRZAVÝ, J., AND V. RIČANKOVÁ. 2004. Phylogeny of recent Canidae (Mammalia, Carnívora): relative reliability and utility of morphological and molecular datasets. *Zoologica Scripta* 33:311–333.
- ZUNINO, G. E., O. B. VACCARO, M. CANEVARI, AND A. L. GARDNER. 1995. Taxonomy of the genus *Lycalopex* (Carnívora: Canidae) in Argentina. *Proceedings of the Biological Society of Washington* 108:729–747.

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