
Taxonomic and biogeographical status of guanaco *Lama guanicoe* (Artiodactyla, Camelidae)

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ABSTRACT

1. We review the status of the four currently recognized guanaco *Lama guanicoe* subspecies, and provide information about their taxonomy and distribution. The success of guanaco in inhabiting open habitats of South America is based mainly on the flexibility of their social behaviour and ecophysiological adaptations to harsh environments.
2. Lönnberg described the first subspecies, *L. g. cacsilensis*, at the beginning of the 20th century. Forty years later Krumbiegel described *L. g. voglii*, based on skull measurements and pelage colouration. The other two subspecies, *L. g. huanacus* and *L. g. guanicoe*, were classified as subspecies by Krumbiegel based on pelage colouration and body size, while maintaining the original Latin names and descriptors.
3. Further guanaco populations have been incorporated into each of these subspecies, based on their proximity to the type locality but without attention to the homogeneity of phenotype or habitat and only limited consideration of Bergmann's rule based on scarce skulls. Two alternative geographical ranges were proposed in the middle and towards the end of the 20th century. Discrepancies occur in the geographical range of each subspecies.
4. Molecular studies based on mitochondrial DNA cytochrome *b* sequences recognized only two subspecies: the Peruvian *L. guanicoe cacsilensis* and the rest of the populations grouped in the clade recognized as *L. g. guanicoe*. We conclude that the evolutionary biology of *L. guanicoe* requires a significant revision with respect to biogeography. Phylogeographical data hold particular value in developing conservation strategies, particularly for some of the reduced and marginal populations and/or subspecies and will support IUCN (The World Conservation Union) Red List classification.

Keywords: conservation, distribution, Guanaco, phenotypes, subspecies

INTRODUCTION

Pigafetta made a description of a strange animal when he arrived in Patagonia with Hernando de Magallanes in 1521. He described a species with a big head and ears like a mule, camel-like neck and body, legs similar to a deer, and tail and alarm calls like a horse (Cabrero, 1985).

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Although early explorers and chroniclers reported guanacos *Lama guanicoe* in these southern latitudes, it was not recognized that the species had a broader distribution in South America (Raedeke, 1979; Franklin, 1982; Torres, 1992; Wheeler, 1995). In fact, the guanaco is found today from Peru (8°S) southward to the central east and western slopes of the Andes, and across Patagonia, including Tierra del Fuego and Navarino Island (55°S; Franklin, 1982; Marchetti, Oltremari & Peters, 1992; Wheeler, 1995). The species inhabits arid, semi-arid, hilly, mountain, steppe and temperate forest environments (Cunazza, 1991). In that wide variety of open habitats, four subspecies of *L. guanicoe* are recognized (Wheeler, 1995): *L. g. cacsilensis* (Lönnerberg, 1913), *L. g. huanacus* (Molina, 1782), *L. g. guanicoe* (Müller, 1776) and *L. g. voglii* (Krumbiegel, 1944).

Recent phylogenetic studies based on anatomy, behaviour and molecular analyses have clearly differentiated the 'guanaco' from its sister taxon *Vicugna vicugna* (the vicuña; Stanley, Kadwell & Wheeler, 1994; Kadwell *et al.*, 2001; Palma *et al.*, 2001). Similarly, its relationship with domestic South American camelids is known from archaeological and molecular remains (Wing, 1986; Stanley *et al.*, 1994; Kadwell *et al.*, 2001). However, at the intraspecific level, both its biogeography and phylogenetic relationships are less clear. Although some guanaco populations have increased in number during the last three decades (Franklin *et al.*, 1997), some populations are endangered, isolated or in restricted areas, such as those in the northernmost and southernmost Peruvian coastal ranges, in the mountains of north and central Chile, in the Bolivian and Paraguayan Chaco, and in the wet and southernmost Navarino Island (Texera, 1973; Torres, 1985; Cunazza, 1991). Therefore, it is important to evaluate the interrelatedness of those populations, to see if they still constitute or are part of the same taxa, and if gene flow continues to link the populations. Such a study would enable appropriate conservation management units to be defined and support conservation policy development.

The purpose of this article is to report what is known and what remains unknown about the four recognized guanaco subspecies, including their taxonomic descriptions and distribution. We begin with general information about guanaco natural history, moving on to consider taxonomy and systematics. Finally, we summarize available information on phenotype and the geographical distribution of each subspecies. This information is crucial as a starting point for advanced research using modern techniques to classify taxonomic units.

NATURAL HISTORY OF THE GUANACO

Origin, evolution and dispersion

The guanaco as a member of the tribe Lamini evolved together with the genera *Palaeolama* and *Vicugna* from the feeder-browser *Hemiauchenia* approximately two million years ago in South America (López Aranguren, 1930; Webb, 1972; Feranec, 2003). Towards the end of the Pleistocene and beginning of the Holocene (13 000–8500 years ago) (Miotti & Salemme, 1999), a massive extinction of megafauna affected both *Hemiauchenia* and *Palaeolama*. The guanaco proved itself as a survivor (Webb, 1978; Markgraf, 1985). Guanacos probably expanded their distribution to include a large part of the southern cone, including high Andes puna (altiplano) (Wheeler, 1995) and Patagonia. Colonization spread to new areas, such as Tierra del Fuego and Navarino islands, using natural land bridges left by the receding glaciers at a time when sea levels were lower than at present (McCulloch *et al.*, 1997; Sarno *et al.*, 2001). During the rest of the Holocene, small climatic changes and human pressure probably affected dispersion of the guanaco, with alternating periods of expansion and colonization events with contraction and extinction of local populations (Miotti & Salemme, 1999; Lepetz, Lefèvre & Pellé, 2003; Barrientos & Perez, 2005). The success of the guanaco to colonize and survive in the open habitats of South America after the Pleistocenic extinction probably

owes much to their flexible social behaviour and ecophysiological adaptations to harsh environments.

Social behaviour and reproductive strategies

The guanaco is a social ungulate that is found in three basic social units during the breeding season: territorial family harems, non-reproductive male groups and solitary males (Franklin, 1982). Outside the breeding season, guanaco group composition varies according to environmental conditions. Sedentary populations are observed when weather and forage supply is stable, allowing populations to live in stable territories all year round (Raedeke, 1979; Franklin, 1983). However, during particularly snowy winters with a drastic reduction of food availability, guanaco may disperse to more sheltered areas, losing their territoriality and forming large mixed herds (Franklin, 1983; Ortega & Franklin, 1995; Bank & Franklin, 1998).

Their reproductive strategy is based around resource defence polygyny where an adult male defends a territory with high relative vegetation quality, suitable habitat for copulation and low abundance of predators (Franklin, 1983; Bank, Sarno & Franklin, 2003; Young & Franklin, 2004a). Normally, the size of a guanaco family group varies between five and 13 adult animals with an average of 2.9 young (Puig & Videla, 1995). In some places, such as in Torres del Paine, large herds of 50 females with offspring were observed moving between male territories at the middle to late mating season (Young & Franklin, 2004b). This behaviour may be linked to high population density. Males and females tend to use the same breeding sites in consecutive years in Patagonia. A high proportion of males returned to the same territory up to eight consecutive years (Young & Franklin, 2004a), and adults mate at the same site within the territory (Bank *et al.*, 2003). The guanaco has a strong reproductive seasonality despite having copulation-induced ovulation (Fowler, 1989). The whole reproductive cycle of birth, mating and early lactation coincides with the best environmental conditions during and after the rainy season. The timing of parturition varies with latitude. In the north of Peru, the offspring are born from April to June (Franklin, 1975), while in Chilean Patagonia births are delayed between mid-November and the end of January. In the Bolivian Chaco, between June and August is the main birth season (WCS, 2004), while on the arid coast of northern Chile, it is possible to see neonates the whole year round, though births are more common between July and December (B. González, unpublished data). In the Andes of northern Chile, newborns begin to appear in August, but they are concentrated between November and February (B. González, unpublished data). It has been reported that in Torres del Paine National Park, 49% of births occur in early December (Garay *et al.*, 1995) and in Tierra del Fuego from mid-December to late February, with 85% of the births between mid-December and late January (Raedeke, 1979).

After 11.5 months of gestation, a female guanaco gives birth to a single offspring that is about 10% of the mother's weight (Sarno & Franklin, 1999a). Births occur during the day in Patagonia with 78% of births being between 10:00 and 14:00 h (Franklin & Johnson, 1994), when the young are able to dry during the favourable temperature conditions of midday. The effect of concentrating births during the day and in only a few weeks in the season is an antipredator strategy, producing an unlimited abundance of prey for pumas *Puma concolor* during a short period (Franklin *et al.*, 1999). Weight at birth is between 7 and 15 kg (Franklin & Johnson, 1994) and shows marked density dependence, with lower birth weights at higher population densities (Sarno & Franklin, 1999b). Low weight at birth is related to high rates of mortality (Gustafson *et al.*, 1998). Neonates have follower behaviour, being able to stand up as early as 5–76 minutes post partum (Franklin & Johnson, 1994; Sarasqueta & de Lamo, 1995). Mothers exhibit aggressive behaviour towards predators. Intensity of defence and

winter snowfall increases survival of neonates to 7 months of age (Sarno *et al.*, 1999). Predation, starvation in winter and accidents are the main causes of mortality during the first year of life, reaching values as high as 70% (Gustafson *et al.*, 1998; Sarno *et al.*, 1999). Because winter is a big challenge for the young, they must grow fast immediately after birth. Forage intake begins as early as 2–4 weeks of age. The response is a high growth rate during the first month of life with weight gain decreasing over time up to the following spring. The young stay with mothers for 1 year, with the males being expelled aggressively from adult male territories before the females, despite their young submissive behaviour (Franklin, 1983; Sarno *et al.*, 2003). The forced dispersal of juvenile guanacos by territorial males is related ultimately to competition for food resources on territories, while sex and time of dispersion are related to future reproductive performance (Sarno *et al.*, 2003). Females reach maturity at 2 years old, and males at 3 years old. The males are able to defend a territory only when fully grown, after 3–4 years old (Raedeke, 1979; Young & Franklin, 2004a).

Foraging behaviour and nutritional strategies

The guanaco may be classified as an intermediate herbivore or opportunistic (mixed) feeder (Hofmann, 1989) foraging on a highly diverse range of food sources, possibly as 'forced selectors' (Puig *et al.*, 1996; Puig, Videla & Cona, 1997; Puig & Videla, 2000). The herbaceous vegetation stratum is the main forage source during the year, with preferences displayed for some plant species (Puig *et al.*, 1997; Puig & Videla, 2000). Nevertheless, when the availability of herbaceous strata decreases during winter, the guanaco feed mainly on the shrub or tree strata (Raedeke, 1979; Bahamonde, Martin & Pelliza Sbriller, 1986; Puig *et al.*, 1996; Puig *et al.*, 1997). This flexibility to change diet according to availability or preference extends to the consumption of lichens and succulent plants (e.g. cactus) in the arid coast of the Atacama Desert (Raedeke & Simonetti, 1988) and to the tree leaves of the deciduous Magellanic forest (Martínez-Pastur *et al.*, 1999; Cuevas, 2002; Cavieres & Fajardo, 2005). In mountainous zones of north-central Chile, the guanaco behaves as a specialized herbaceous feeder, probably due to the low palatability of native plants (Cortés *et al.*, 2003). The main adaptations that the camelid family have in terms of their digestive physiology are an increased ability to digest low-quality forage by prolonging the particle retention time in the pseudo rumen and a high efficiency in the use of water, especially when there is low food intake (Engelhardt *et al.*, 1991). Foraging behaviour and digestive adaptations to harsh environments have allowed the guanaco to become the dominant large herbivore of the scrubland and steppes of South America.

Habitats and threats

Raedeke (1979) estimated the total guanaco population at the time when Europeans arrived on the new continent at between 30 and 50 million animals. The guanaco inhabits environments characterized by highly seasonal weather, with snow cover or dry winters, cold to freezing temperatures, moderate to high winds and precipitation which combine to produce high evapo-transpiration and dry conditions and lead to low primary productivity (Franklin, 1983). These environments are found in most biomes of the Patagonian subregion (Hershkovitz, 1972). At a broad scale, guanacoes inhabit four of the 10 major habitats described in South America: (i) desert and xeric shrublands; (ii) montane grasslands; (iii) grasslands, savannas and shrublands; and (iv) temperate forests (Dinerstein *et al.*, 1995).

Deserts and xeric shrublands are located at the western slope of the Andes and include the arid desert ecoregions of South America. Montane grasslands include areas influenced by the Andes mountains in Peru, Bolivia, Argentina and Chile, including central Andean dry

puna, southern Andean steppe, Patagonian Steppe and Patagonian grassland ecoregions. The grasslands, savannas and shrublands include arid environments at the eastern slope of Andes across Bolivia, Paraguay and Argentina including the Chaco savanna, Argentine monte and Argentine espinal ecoregions. Finally, temperate forests only include the subpolar *Nothofagus* forest ecoregion at the southernmost part of South America (Dinerstein *et al.*, 1995). Guanaco populations are extinct in the Chilean matorral ecoregion (Miller, 1980).

The deserts of coastal Peru and northern Chile form a continuous belt along the western escarpment of the Andean cordillera for more than 3500 km from the Peru/Ecuador border (5°00'S) to northern Chile (29°55'S). Seasonal fog allows for the development of rich fog-zone vegetation, termed *lomas* formations ('small hills'). Native vegetation of the deserts consists of many highly endemic and largely restricted to the fog-zone (Rundel *et al.*, 1990). The floristic communities of the *lomas* formations essentially function as terrestrial islands separated by hyperarid habitat where virtually no plants exist (Rundel *et al.*, 1990). Guanacos inhabit that environment at low densities surviving on this particular vegetation (Raedeke & Simonetti, 1988; Cunazza, 1991).

Montane grasslands are constituted by the puna (or altiplano), the pre-puna as well as the Patagonian Steppe. The puna is located between 15° and 27°S latitude, at an elevation that fluctuates between 3800 and 4500 m in the central cordillera of the Andes of South America. In some parts of that area small guanaco populations overlap with more abundant vicuña (Lucherini, 1996; Rundel & Palma, 2000). This biome is characterized by having a mean annual precipitation of 150–230 mm and vegetation composed of steppe grasses such as *Festuca* and *Stipa* (Negrete-Córdova, 1997). Between 3200 and 3800 m, the regime of precipitation decreases between 70 and 150 mm with the characteristic tolar shrubs (e.g. *Parastrephia* spp., *Chuquiraga* spp.), some columnar cacti and summer annual plants (Kalin-Arroyo *et al.*, 1997). The pre-puna, on the other hand, is located between 2600 and 3200 m and the mean annual precipitation ranges from 20 to 70 mm supporting salt tolerant shrubs (*Atriplex*), cushion cacti (*Opuntia*) and a few annual plants (Negrete-Córdova, 1997). At these altitudes, guanacos are sympatric with highly restricted populations of Andean huemul *Hippocamelus anticensis* (Rundel & Palma, 2000). At lower elevation, the pre-puna gives way to the Atacama Desert, a barren landscape that lacks vegetation because of decades without any rain. Finally, the Patagonian Steppe mainly covers the Patagonia region of Argentina from the Atlantic Ocean shore across the border into Chile. The topography of this ecoregion includes low-lying mountains, plateaus and plains. Soils are variable but generally rocky-sandy and poor in fine materials and organic matter. The climate is very dry and cold with snow during the winter and frosts nearly year-round, although annual precipitation is no more than 200 mm. The vegetation of the Patagonian Steppe is xerophytic and highly adapted to resist drought, wind and herbivores such as guanacos (Franklin, 1982; Torres, 1992).

The Chaco ecoregion is generally restricted to the north-western two-thirds of western Paraguay, and east of the Andes in south-eastern Bolivia and north-western Argentina (Olson *et al.*, 2000). The northern, southern, western and eastern boundaries of this ecoregion terminates approximately at 17° and 31°S and 61° and 65°W, respectively (Roig & Flores, 2001). Mean annual temperature in the central Paraguayan Chaco during 1980–90 was 26 °C and annual rainfall was 865 mm (Brooks, 1993). Dominant species include *Prosopis ruscifolia*, a thorny legume, and *Opuntia* sp. a cactus (López *et al.*, 1987). The understory of primary thorn forest is punctuated with spiny terrestrial plants such as bromeliads *Bromelia serra* and star cactus *Cleistocactus baumanii* (Roig & Flores, 2001). The guanaco is considered near extinction in the Chaco (WCS, 2004). The monte, on the other hand, is restricted to Argentina

from 24° to 43°S. Its landscape is mostly sandy plants, plateaus and mountain bases. Annual rainfall ranges from 80 to 200 mm, and the annual mean temperature ranges from 13 °C to 15.5 °C (Roig-Juñent *et al.*, 2001). This is defined as a xeric biome according to its vegetation and physiognomy (Cabrera, 1953; Morello, 1958; Roig, 1998). There are also edaphic communities of many species such as woods of the genus *Prosopis*, shrubs of *Baccharis* in humid places and *Atriplex* in clayish soils (Roig-Juñent & Flores, 2001). Isolated and small-size guanaco populations are recorded for this ecoregion (Sosa & Sarasola, 2005).

The temperate forests are inhabited by guanacos only on its southernmost distributional range, particularly from Tierra del Fuego to Navarino Island (Texera, 1973). These areas are characterized by heavy winds with annual precipitation rate of about 750 mm. Besides the maritime influence of the area, winter temperature can be as low as 12 °C below zero, whereas the highest temperatures can reach up to 31 °C during summer. These forests are also characterized by the presence of deciduous forms such as 'lenga' *Nothofagus pumilio* and 'ñirre' forests *N. antarctica*, as well as coastal evergreen forests such as 'coigüe de Magallanes' *N. betuloides* and 'canelo' *Drymis winteri* (Veblen, Schlegel & Oltremari, 1983). Wide meadows are characteristic in humid areas. The guanaco use this ecoregion from coastal beaches to rocky zones as well as vegetation over the forest line (Massoia & Chevez, 1993).

Throughout its distribution, the guanaco is an important species in maintaining ecosystem function, controlling vegetation growth, dispersing seeds and contributing to the food chain in every ecoregion it inhabits. Studies summarized by Fuentes & Muñoz (1995) indicate that the guanaco, as a native herbivore in central Chile, probably maintained plant cover and composition of Mediterranean vegetation. On the other hand, guanaco dung heaps are a highly nutritive stratum for undigested seeds or to those dispersed by wind in resource-poor environments accelerating the process of plant colonization (Henríquez, 2004). Finally, guanaco is the main prey for pumas in the Andes mountains and some parts of Patagonia, except Tierra del Fuego and Navarino islands, where these felids do not occur (Texera, 1973; Wilson, 1984; Iriarte, Franklin & Johnson, 1991; Bank & Franklin, 1998; Cajal & López, 1998; Franklin *et al.*, 1999; Bank *et al.*, 2002) and their carcasses supply food for carrion-eaters like foxes (Chilla fox *Lycalopex griseus*, and Culpeo fox *Lycalopex culapeus*) and birds of prey (Crested caracara *Polyborus plancus*, and Andean condor *Vultur gryphus*) (Johnson & Franklin, 1994; Sarno, Franklin & Prexl, 2000; Travaini *et al.*, 2001).

During the last century, guanaco populations have decreased in number to no more than one million animals and their distribution has declined by 60% (Puig & Rabinovich, 1995). High competition for forage with sheep, goats, horses, donkeys and cattle and predation by feral dogs are consequences of sympatry between humans and guanaco throughout the species' range (Raedeke, 1982; Puig *et al.*, 2001; Baldi *et al.*, 2004). Intensification of farming and livestock herding have reduced available habitat and hunting pressure has impacted on many populations (Raedeke, 1979; Franklin *et al.*, 1997; Donadio & Buskirk, 2006). Decreasing guanaco numbers reduced the ecological functions of guanaco in the ecosystems. Pumas, for example, have tended to switch from native prey to more abundant small native prey or domestic or exotic animals (Novaro, Funes & Walker, 2000; Sosa & Sarasola, 2005) while herbivores introduced to Mediterranean ecosystems have affected plant cover, species composition and shrub seedling recruitment (Fuentes & Muñoz, 1995).

SYSTEMATICS OF GUANACO *LAMA GUANICOE* (MÜLLER, 1776)

Müller recognized the guanaco as a species in 1776. Initially, he named it as '*Camelus guanicoe*'. Later, in 1782, Molina described its morphology, behaviour and its use by humans, naming it '*Camelus huanacus*'. This discrepancy in nomenclature confused some subsequent

investigators and Osgood (1943) used the name *guanicoe*. A synonymy of guanaco and its subspecies is provided in Table 1.

Guanaco subspecies have been described based on body size, skin colour, skull size and skull proportions. The first attempt to describe different guanaco subspecies was conducted by Lönnberg (1913) who characterized one specimen from the Peruvian mountains as having a small skull size when compared with specimens from Patagonia and Tierra del Fuego, naming it '*Lama huanachus cacsilensis*'. Krumbiegel (1944) agreed with the new taxon and added a new subspecies based on colour, body size and skull measurements. He named these new taxa '*Lama guanicoe voglii*'. The latter author also compared skull measurements of guanacos from different populations in South America, adding two taxa: '*Lama guanicoe*

Table 1. A revised synonymy of guanaco

Scientific name	Reference (according to Osgood 1943 and Cabrera 1961)
<i>Camelus guanicoe</i>	Müller (1776) <i>Linné Natursyst.</i> p. 50, Suppl. – Patagonia.
<i>Camelus huanacus</i>	Molina (1782) <i>Sagg. Stor. Nat. Chili.</i> p. 317 – Chile.
<i>Camellus huanacus</i>	Molina (1788) <i>Comp. Hist. Nat. Chile.</i> p. 360 – Chile.
<i>Auchenia huanaco</i>	Von Tschudi (1846) <i>Fau. Peruana.</i>
<i>Camelus guanaco</i>	Traill (1820) <i>Mem. Werner. Soc. Nat. Hist.</i> 4, p. 492, Fig.
<i>Lama peruviana</i>	Lesson (1827) <i>Man. de Mammal</i> p. 352 (parte).
<i>Auchenia huanaca</i>	Hamilton Smmith (1827) in Griffith, <i>Anim. Kingd.</i> 5, p. 299.
<i>Lama peruana</i>	Fischen (1829) <i>Syn. Mammal</i> p. 436.
<i>Auchenia guanaco</i>	Meyen (1833) <i>Nov Act. Acad. Leop.</i> – <i>Carol. Nat. Curios.</i> 16, pt. 2. 552, pl. 40.
<i>Auchenia llama</i>	Waterhouse (1838) <i>Zool. Voy. Beagle</i> p. 26, 1839.
<i>Auchenia lama</i> , a. <i>guanaco</i>	Wagner (1839) <i>Schreibers Säught.</i> Suppl. 5, p. 1803.
<i>Lama pacos (fera)</i>	Gray (1843) <i>List. Mamm. Brit. Mus.</i> p. 171.
<i>Lama molinaei</i>	Boitard (1845) <i>Jard. des Plant.</i> p. 426.
<i>Auchenia guanacos</i>	Schinz (1845) <i>Syst. Verz. Säugeh.</i> p. 366.
<i>Auchenia lama</i>	Brandt (1845) <i>Mém. Acad. Scienc. St. Pétersb.</i> 4, p. 1 (no Illger 1811).
<i>Lama guanaco</i>	Gay (1847) <i>Hist. Chile, Zool.</i> 1, p. 153.
<i>Lama huanacus</i>	Gray (1830) <i>Glean. Menag. Knowsley.</i>
<i>Llama guanacus</i>	Gray (1852) <i>Catal. Specim. Mamm. Brit. Mus.</i> 3, p. 257 (lám. 24, f. 1).
<i>Palaeolama mesolithica</i>	Gervais & Ameghino (1880) <i>Mamm. Fos. Amér. Sud.</i> p. 120.
<i>Lama huanachus</i>	Thomas (1891) <i>Proc. Zool. Soc. Lond.</i> p. 387.
<i>Auchenia huanacus</i>	Flower & Lydekker (1891) <i>Introd. Study Mamm.</i> p. 300.
<i>Lama huanacos</i>	Slater (1891) <i>Proc. Zool. Soc. London</i> p. 669.
<i>Auchenia Lönnbergi</i>	Ameghino (1899) <i>Sinops. Geol. – Paleont. Patag.</i> Suppl., p. 6.
<i>Lama huanacha</i>	Elliot (1907) <i>Field Mus. Nat. Hist.</i> 8, p. 36.
<i>Lama huanachus cacsilensis</i>	Lönnberg (1913) <i>Arkiv. Zoologi.</i> 8, p. 8.
<i>Lama glama huanacus</i>	Lydekker (1915) <i>Catal. Ungul. Brit. Mus.</i> 4, p. 302.
<i>Lama glama cacsilensis</i>	Lydekker (1915) <i>Catal. Ungul. Brit. Mus.</i> 4, p. 304.
<i>Lama guanicoe</i>	Osgood (1921) <i>Journ. Mamm.</i> 2, p. 39.
<i>Lama guanicoe cacsilensis</i>	Osgood (1921) <i>Journ. Mamm.</i> 2, p. 39.
<i>Auchenia guanicoe</i>	Housse (1929) <i>Rev. Chil. Hist. Nat.</i> p. 38 – Chile.
<i>Lama guanicoe guanicoe</i>	López Aranguren (1930) <i>Anal. Soc. Cient. Arg.</i> 109, p. 106. Krumbiegel (1944) <i>Zoolog. Anzeig.</i> 145, p. 56.
<i>Lama guanicoe lönnbergi</i>	López Aranguren (1930) <i>loc. Cit.</i> p. 39.
<i>Lama guanicoe</i>	Cabrera (1932) <i>rev. Mus. La Plata</i> 33, p. 116.
<i>Lama glama huanacus</i>	Allen (1942) <i>Ext. & Vanish. Mamm. West. Hemisph.</i>
<i>Lama guanicoe voglii</i>	Krumbiegel (1944) <i>Zoolog. Anzeig.</i> 145, p. 56.
<i>Lama guanicoe huanacos</i>	Krumbiegel (1944) <i>Zoolog. Anzeig.</i> 145, p. 56.
<i>Lama guanicoe cacsilensis</i>	Krumbiegel (1944) <i>Zoolog. Anzeig.</i> 145, p. 56.

Reference is cited only if it appears in the main text.

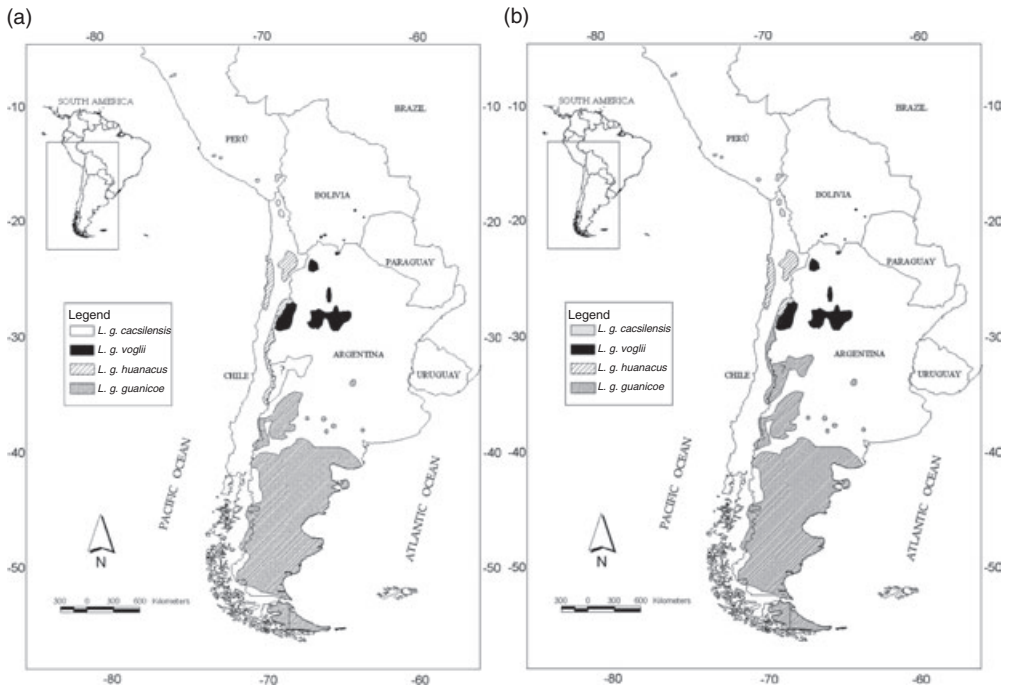


Fig. 1. (a) Distribution of guanaco subspecies according to Krumbiegel (1944), and (b) according to Wheeler (1995). Note that no guanaco population from central west Argentina is included in the map (a), while *L. g. huanacae* is only restricted to northern Chile in map (b). Map adapted from Torres (1992).

guanicoe' and '*Lama guanicoe huanacos*' and described their general range of distribution (Fig. 1a). Herre (1952) pointed out that size differences among subspecies were related to Bergmann's rule, but Franklin (1982) suggested that more studies were necessary to support this biogeographical hypothesis. On the other hand, Dennler de la Tour, 1954) and Cabrera (1961) recognized only two subspecies: *L. g. cacsilensis* in the Peruvian Andes, and *L. g. guanicoe* 'in other areas' (without specification of what 'other areas' meant). Wheeler (1995) associated the four described subspecies with the range of distribution given by Krumbiegel (1944) and population clusters compiled by Torres (1992), and proposed a new distribution as shown in Fig. 1b. This was the first attempt to describe the guanaco's zoogeography, though the author herself emphasized the lack of information to support this hypothesis.

***Lama guanicoe cacsilensis* (Lönnberg 1913)**

History

Lönnberg (1913) carried out comparative morphological studies between Patagonian guanaco skulls ($n = 3$) and one specimen collected in a Peruvian Andean zone called Cacsile (Departamento de Puno). He suggested that this specimen constituted a local race and classified it as *Lama huanachus cacsilensis*. The Cacsilian skull was smaller than those of the Patagonian specimens; however, the age and sex of the specimen were not reported. This subspecies was later recognized by Osgood (1916) near Arequipa, based on specimens collected during the 'Collins – Day South American Expeditions' survey. Osgood also indicated that his study suffered from a lack of samples (he did not give the exact number of specimens).

In a separate study, León (1933; cited by Krumbiegel, 1944; MacDonagh, 1949 and Herre, 1952) proposed this subspecies as a hybrid between guanaco and vicuña. This was criticized by Herre (1952) who argued that there was a lack of evidence to support this conclusion.

Phenotype

L. g. cacsilensis has been characterized by its smaller body and skull size, as compared to other guanaco subspecies (Osgood, 1916; Krumbiegel, 1944; Franklin, 1982; Wheeler, 1995). Wheeler (1995), citing Herre (1952, p. 73), indicated a wither height of 100 cm, without specifying either the origin or age of specimens. The body length measured from the tip of the nose to the base of the tail varied between 90 and 100 cm for specimens from Calipuy, north-west Peru (Kostrisky & Vílchez, 1974). Since these measurements are similar to or even smaller than those typical of vicuñas (Wheeler, 1995), it seems probable that these measurements were from a juvenile animal. In fact, Von Tschudi (1846) recorded the body weight of a Peruvian male (near Puno) of 96 kg and a length of 219 cm – dimensions similar to Patagonian guanacos (Lönnerberg, 1913; Kostrisky & Vílchez, 1974).

L. g. cacsilensis has a smaller skull size and different cranial proportions than the Patagonian populations. Lönnerberg (1913) reported skull dimensions of 261 mm long by 128 mm wide for this taxon and recorded that the pre-orbital area was 33% of the total skull length, while Krumbiegel (1944) reported a value of 48%. Despite these differences, both measurements are below the 49–53% range of *L. g. guanicoe* skulls from Patagonia. Lönnerberg (1913) observed that Peruvian guanacos were similar in colour to southern populations, though Wheeler (1995) describes them as light brown with ochre yellow colouration.

Distribution

Populations in Peru, northern Chile and sometimes Bolivia have historically been classified as *L. g. cacsilensis* (Osgood, 1916; Krumbiegel, 1944; Cabrera, 1961; Franklin, 1982; Torres, 1985). Osgood (1916) did not observe guanacos to the north of Arequipa, Peru. The current northern limit for this subspecies is the area of Calipuy, Peru (8°S, Grimwood, 1969; Franklin, 1975), although Paucar (1992) reported possible hybrid descendants of guanacos and llamas in Ecuador. Torres (1985) indicated that the southern limit of this subspecies is probably the northern part of Chile. Wheeler (1995) recognized the distribution of the subspecies *L. g. cacsilensis* between 8° and 22°S, based on contemporary data of guanaco populations reported by Torres (1992). She also established that the populations of this taxon occur predominantly at higher elevations, although in Pampa Galeras (Ayacucho, Peru) they descend to the coast, mainly due to human disturbance. Grimwood (1969) reported that guanacos were to be found mainly on the upper slopes of mountains, but that they appear on the coastal plains during winter. He also described the Peruvian guanaco as a rare species in danger of extinction.

***Lama guanicoe voglii* (Krumbiegel 1944)**

History

Krumbiegel (1944) proposed this subspecies for northern Argentinean populations, based on colour pattern and its smaller and less robust body compared to the Patagonian guanaco. He named it *Lama guanicoe voglii* in honour of the priest Cornelius Vogl, although the scarcity of material made it difficult to produce a detailed description. His samples came from Sierra de Lípez and Uyuni in Bolivia. Cabrera (1961) criticized the description of the distribution in northern Argentina, giving three alternative classifications: (i) if this population is not phylogenetically distinct from northern Chilean populations, then it should be recognized

as *Lama guanicoe huanacus*; (ii) if the population is a different subspecies, it should be recognized as *L. g. mesolithica* based on a camelid fossil from Buenos Aires, Argentina; and (iii) if the Argentinean specimens are not different from *L. g. guanicoe*, they should have the synonym *molinaei*.

Phenotype

There is little information about body measurements. Herre (1952) hypothesized that *L. g. voglii* should be smaller than the southern forms, but Cardozo (1954) reported an individual in Bolivia whose length, 215 cm, was similar to that of the Patagonian guanaco. Krumbiegel (1944) reported wither height as 100–108 cm, with a pearl to light grey colouration on the cheeks and nape. The pelage is brownish yellow, in contrast to the brownish red of the Patagonian guanaco. The skull dimensions given by Krumbiegel (1944) are 280 mm long by 140 mm wide. Current phylogenetic and morphological studies of this subspecies are not available. However, it is clear that the low population is at serious risk of extinction (Ríos, 1992; Cuellar & Fuentes, 2000).

Distribution

Krumbiegel (1944) commented that *L. g. voglii* ranged from 33°S northward and bordered with the Andes mountains to the west. He also suggested that populations in La Rioja, Argentina corresponded to this subspecies. Wheeler (1995) stated that this form is distributed between 21° and 32°S on the eastern slopes of the Argentinean Andes, although Franklin (1982) extended its distribution north beyond 32°S through the arid areas and plains of Argentina and possibly Paraguay.

***Lama guanicoe guanicoe* (Müller, 1776)**

History

Krumbiegel proposed this subspecies, described in the literature as the Patagonian race or 'large race', in 1944, as it differed from the previously recognized *L. g. voglii* and *L. g. cacsilensis* subspecies. Krumbiegel maintained the original classification of *guanicoe* given by Müller in 1776, possibly because he was working with specimens from Patagonia (Müller did not mention the origin of the material). However, in 1930, Dolores López Aranguren had already given the name *Lama guanicoe guanicoe* to a new species of a Pleistocene camelid fossil from Argentina. Fortunately, the extinct species and subspecies described by Krumbiegel in 1944 were found later to be the same.

Phenotype

Several authors considered that, in general, members of the subspecies *L. g. guanicoe* are larger than other members of *Lama guanicoe* (Lönnberg, 1913; Krumbiegel, 1944; Herre, 1952; Wheeler, 1995). Information about wither height indicated values between 110 and 125 cm (Krumbiegel, 1944; MacDonagh, 1949; Dennler de la Tour, 1954; Cabrera & Yepes, 1960; Raedeke, 1979). The total length (tip of the nose to the base of the tail) varied between 152 and 215 cm (Allen, 1905; MacDonagh, 1949; Dennler de la Tour, 1954; Cabrera & Yepes, 1960; Raedeke, 1979). The weight of mature animals is 120.2 ± 12.2 kg in Tierra del Fuego (Raedeke, 1979), and reached 80 kg in northern Patagonian populations (Puig & Monge, 1983; Puig *et al.*, 2001). Individuals in the Atlantic coastal populations weighed between 90 and 105 kg (Romero, 1927; de Lamo, 1990). Osgood (1943) and MacDonagh (1949) reported a difference in size between the populations on the mainland of southern South America, the Island of Tierra del Fuego, and Navarino Island, with the latter being larger.

Krumbiegel (1944), after analysing skull measurements, determined that the skull length of an adult specimen of *L. g. guanicoe* ranged from 286 to 310 mm, the width from 135 to 152 mm, and that the pre-orbital area was between 49% and 53% of the total skull length. Current studies among populations of the same subspecies from Torres del Paine National Park (Chilean Patagonia), Tierra del Fuego and the Falkland Islands have indicated a homogeneity in size, although the population on the Falkland Islands may have on average a smaller skull length (J. Donnelly, personal communication). This study did not include skulls from northern populations of the subspecies.

Pelage colouration for *L. g. guanicoe* is brownish red on the trunk and neck, while the head, cheeks and nape are light grey (Krumbiegel, 1944; Wheeler, 1995). There are differences in colour between populations. MacDonagh (1949) indicated that the specimens obtained in Curámatal, Province of Buenos Aires, Argentina possess a cinnamon rufous half-line on the dorsum, with clearer sides, while the abdomen has a dirty white colouration. The Patagonian continental populations are brown and slightly reddish, while those of Tierra del Fuego are dark reddish. Reynolds (1957) recorded the existence of three varieties of Fueguinean guanacos based on the colouration and length of the hair. Guanacos from the steppes located to the north of the Magellan Straits have a short, yellowish coat, while guanacos from the forested and mountainous areas in southern Tierra del Fuego have a long coat and reddish brown colour. The endemic populations of Navarino Island have a long shiny coat.

Distribution

There is some confusion in establishing the distributional limits of this subspecies. Krumbiegel (1944) indicated that the distribution of *L. g. guanicoe* ranges from Patagonia and Tierra del Fuego up to a northern limit of 35°S and considered the populations from Buenos Aires as the northernmost populations of the Patagonian subspecies. Torres (1992) mentioned that *L. g. guanicoe* also inhabits Chile and Argentina up to a northern limit of 38°S. Wheeler (1995) reported that this taxon extends from the western slope of the Andes throughout Patagonia from 32° to 55°S. The presence of this species in insular areas (the Island of Tierra del Fuego and Navarino Island) has prompted some authors to propose a dispersal scenario including colonization by swimming (Darwin, 1839; Dennler de la Tour, 1954) and/or introduction by humans (Osgood, 1916). Molecular studies that attempt to estimate a probable colonization date have indicated that the entrance of guanacos to Tierra del Fuego may have occurred approximately 8000 years ago, when this island was still linked to the continent during the last glacial cycles of the Pleistocene (MacCulloch *et al.*, 1997; Sarno *et al.*, 2001). A herd of guanaco introduced during the 1930s from southern Patagonia survives in Falkland Islands despite a reduced gene pool, population bottlenecking and inbreeding (Franklin & Grigione, 2005; Franklin, Poncet & Poncet, 2005).

***Lama guanicoe huanacus* (Molina 1782)**

History

Krumbiegel (1944) based his proposition of this subspecies on a difference in colouration pattern with respect to Patagonian specimens. He recognized it as a geographical variety for Chile based also on size given by Molina (1782). Krumbiegel (1944) retained the name '*huanacus*' assigned by Molina to populations of central Chile, although he misspelled it as '*huanacos*'.

Phenotype

Krumbiegel (1944) did not find significant differences in cranial and general measurements when comparing this subspecies with some of the other forms, including it within 'the big



Fig. 2. Juveniles of *Lama guanicoe huanacus* (Molina, 1782) according to Krumbiegel (1944) or *Lama guanicoe guanicoe* (Müller, 1776) according to Wheeler (1995) in Andes mountains, north-central Chile (31°71'S). Photo by Benito A. González.

forms' close to *L. g. voglii* and *L. g. guanicoe*. Molina (1782) gave the following dimensions for this guanaco subspecies: wither height 111 cm; total length 210 cm (possibly considering the tail). Additionally, Krumbiegel (1944) indicated a wither height of 92–122 cm. Skulls analysed by this author from northern and central Chile gave measurement of 260–292 mm long, and 140–146 mm wide.

Molina (1782) did not detail the pelage colouration of the Chilean guanaco, only mentioning that it has reddish back and dirty white ventral parts. Herre (1952) indicated that the colouration of the body is dark brown, and that this colouration extends also to the head and neck. Krumbiegel (1944) gave more details describing this form as having a grey head, being almost black in colour, with darker grey cheeks and a grey to black nape and neck, extending to just behind the ears.

Distribution

The distribution of *L. g. huanacus* is ambiguous, although it is restricted to Chile. Franklin (1982) specified that this form inhabits the western slopes of the Andes. Wheeler (1995) restricted its distribution in Chile between 22° and 28°S, recognizing all populations south of 28°S as *L. g. guanicoe* (Fig. 2). The lack of precision and the non-existence of a holotype were criticized by Krumbiegel (1944) who only had access to specimens from Tocopilla, Atacama and the mountains around Santiago in northern and central Chile, respectively.

DISCUSSION

Four guanaco subspecies have been described in the past on the basis of skull measurements, body size and pelage colouration. Nevertheless, these morphological traits have not allowed

Table 2. Main phenotypic descriptions of *Lama guanicoe* subspecies including values, specimens age and sample size

Character	Subspecies	Value	Age	No.	References
Body length (cm) (from tip of the nose to base of the tail)	<i>L. g. cacsilensis</i>	90–130	Juv.?	3?	Osgood (1916); Kostrisky & Vílchez (1974)
		219*	Ad.	1	Von Tschudi (1846)
	<i>L. g. huanacus</i>	210	Ad.	?	Molina (1782)
	<i>L. g. voglii</i>	215	Ad.	?	Cardozo (1954)‡
	<i>L. g. guanicoe</i>	152–215	Ad.	–	Any authors (see text)
Withers height (cm)	<i>L. g. cacsilensis</i>	100	Ad.	?	Wheeler (1995)
	<i>L. g. cacsilensis</i>	99	Ad.	1	Von Tschudi (1846)
	<i>L. g. huanacus</i>	111	Ad.	?	Molina (1782)
	<i>L. g. voglii</i>	100–108	Ad.	3	Krumbiegel (1944)
	<i>L. g. voglii</i>	111	Ad.	?	Cardozo (1954)‡
	<i>L. g. guanicoe</i>	110–125	Ad.	–	Any authors (see text)
Live weight (kg)	<i>L. g. cacsilensis</i>	96	Ad.	?	Kostrisky & Vílchez (1974)
	<i>L. g. huanacus</i>	100?	Ad.	?	Herre (1952)
	<i>L. g. voglii</i>	48	Juv.?	?	Cardozo (1954)‡
	<i>L. g. guanicoe</i>	120.2	Ad.	19	Raedeke (1979)
	<i>L. g. guanicoe</i>	90–100	Ad.	7	de Lamo (1990) (northern Patagonia)
Chest girth (cm)	<i>L. g. cacsilensis</i>	108	Ad.	?	Osgood (1916)
	<i>L. g. guanicoe</i>	110.3	Ad.	23	Raedeke (1979)
	<i>L. g. guanicoe</i>	123	Ad.	?	Allen (1905)
Skull length (mm)	<i>L. g. cacsilensis</i>	261	Ad.	1	Lönnberg (1913)
	<i>L. g. cacsilensis</i>	290†	Ad.	1	Von Tschudi (1846)
	<i>L. g. huanacus</i>	260–292	Ad.	4	Krumbiegel (1944)
	<i>L. g. voglii</i>	280	Ad.	4	Krumbiegel (1944)
	<i>L. g. guanicoe</i>	286–310	Ad.	29?	Krumbiegel (1944)
Skull width (mm)	<i>L. g. cacsilensis</i>	128	Ad.	1	Lönnberg (1913)
	<i>L. g. huanacus</i>	140–146	Ad.	4	Krumbiegel (1944)
	<i>L. g. voglii</i>	140	Ad.	4	Krumbiegel (1944)
	<i>L. g. guanicoe</i>	135–152	Ad.	29?	Krumbiegel (1944)
Pelage colour (head colour is given where different)	<i>L. g. cacsilensis</i>	Light brown with ochre yellow tones			Wheeler (1995)
	<i>L. g. huanacus</i>	Dark brown; black head			Krumbiegel (1944); Herre (1952)
	<i>L. g. voglii</i>	Yellowish brown to sandy			Krumbiegel (1944)
	<i>L. g. guanicoe</i>	Dark reddish brown; grey head			Krumbiegel (1944); Wheeler (1995)

Ad., Adult; Juv., Juvenile.

*Estimated from head, neck and trunk lengths.

†Head length, not skull length.

‡Probably near Lake Titicaca, Bolivia (cited by Raedeke, 1979).

a clear distinction between these subspecies (Table 2). The description of subspecies has been based on few specimens. In fact, *Lama guanicoe cacsilensis* was described using just one skull while the descriptions of *Lama guanicoe huanacus* and *L. g. voglii* were based upon four skulls. However, better sample sizes were used to describe the Patagonian *L. g. guanicoe*, for which 30 skulls were used (Krumbiegel, 1944). Body length, wither height, live weight and chest girth were recorded in some cases from an unknown number of specimens without information about their exact age, locality, etc., as is recommended (Bisby, 1995). This lack of rigour

in early descriptions is not surprising, since a great number of neotropical mammals were described in the past following similar criteria. Only during recent decades has it been possible to determine the existence of subspecies with high precision, using several morphological characters and supported with more sophisticated methodological analyses, both statistical and phylogenetic. Other approaches, such as the use of molecular tools (Molina & Molinari, 1999; Culver *et al.*, 2000; Sarno *et al.*, 2004), have also been increasingly used.

Ecogeographical trends such as Bergmann's rule (Mayr, 1956), reflected in skulls and body measurements, are mentioned in most guanaco studies. However, data collected from historical reports do not support this rule. Further investigation is necessary to establish if guanacos show any ecogeographical patterns. Bergmann's rule has recently been criticized and its validity is frequently questioned (Geist, 1987; Ashton, Tracy & de Queiroz, 2000; Meiri & Dayan, 2003) due to the assumptions it makes about thermoregulation and body size and the relationship between environmental temperature and distance from the equator. Nevertheless, some studies reporting body size variations with latitude support this rule. The puma is a good example from among the South American mammals (Iriarte *et al.*, 1990; Gay & Best, 1996). The Andean fox, *Dusicyon culpaeus*, is a neotropical canid that also shows an increase in size with latitude, but this feature has been attributed to size of potential prey and competition more than a biogeographical rule (Fuentes & Jaksic, 1979).

Spatial limits defined for each subspecies are not clear and may not reflect reality. They have been defined while assuming close correspondence of populations to the specimens on which the classification was based without contrasting samples with the subspecies holotype. In addition, natural borders such as changes in vegetation cover, geographical barriers and climate variations do not explain the borders and differences between subspecies, because they do not produce effective geographical isolation. For example, the Andes mountains have been used as a natural border of distribution between *L. g. huanacus* in Chile and *voglii* in Argentina. This mountain range, however, appears to offer little impediment to movement. Observations of populations that inhabit the mountainous environment in central Chile have recorded movements from one side to the other, according to climatic conditions and food availability (Veloso *et al.*, 2002; Contreras, González & Novoa, 2006). Current distributional discontinuity and isolation of some guanaco populations in mainland South America are historical, and have been the result of recent human activities (Franklin, 1982; Torres, 1985; Marchetti *et al.*, 1992; Torres, 1992).

Phylogenetic studies on South American camelids are still in development. Each taxon is being re-evaluated using well-supported phylogenies, as well as increased sample sizes to evaluate the systematic status of the subspecies of *Lama guanicoe*. Current molecular methods should be allowed to augment traditional taxonomic studies to establish evolutionary history (O'Brien, 1994). This is currently being applied to each of the four species of South American camelids at a broad scale of evolution (Stanley *et al.*, 1994; Kadwell *et al.*, 2001) and at a local scale to evaluate genetic diversity within populations (Sarno *et al.*, 2000; Sarno *et al.*, 2004; Mate *et al.*, 2005). Recent phylogenetic and phylogeographical studies on guanacos based on cytochrome *b* mitochondrial sequences that included all nominal subspecies from different locations in Argentina, Bolivia, Chile and Peru recovered two different lineages: a northern grouping representing *L. g. cacsilensis* populations, and another major clade that comprised the geographical distribution of *huanacus*, *guanicoe* and *voglii* (Fig. 3; Marín, Spotorno & Wheeler, 2006). In fact, the northernmost form *L. g. cacsilensis* was recovered as a differentiated clade with respect to all the southern forms from Bolivia, Argentina and Chile (Marín *et al.*, in press), and it seems like that taxon is the most basal form confirming a northern origin for the species, with subsequent dispersal southward (see below). Thus, the

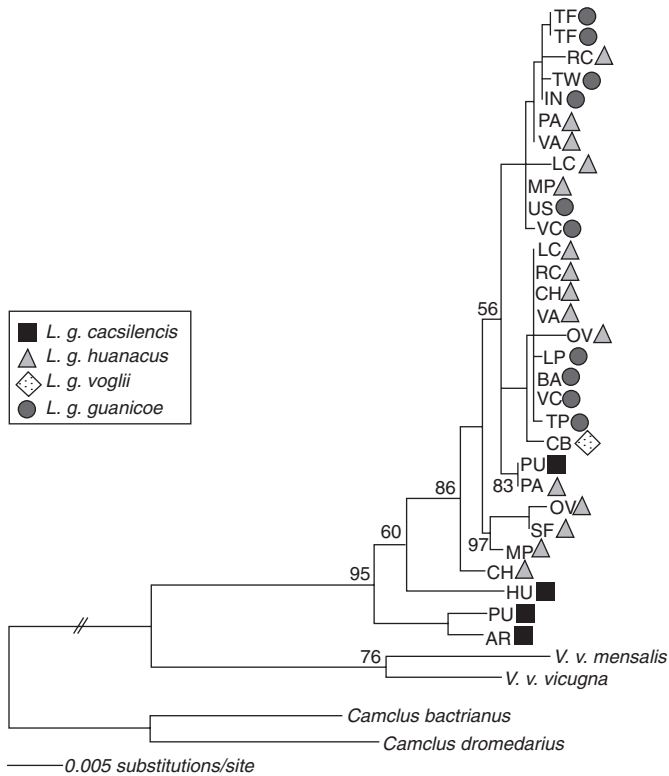


Fig. 3. Phylogenetic relationships among the nominal subspecies of *Lama guanicoe* obtained through maximum likelihood ($-\ln L = 2992.60360$, $t_i : t_v$ ratio = 5.54) based on sequences of the cytochrome b mitochondrial gene (HKY+G model). Bootstrap values (100 replicates; > 50%) are over each node. Abbreviations are square: *Lama guanicoe cacsilensis*, triangle *L. g. huanacus*, rhombus *L. g. voglii* and circle *L. g. guanicoe* (adapted from Marín et al., 2006). Capital letters indicate different localities.

former results recognized the occurrence of the northern form *L. g. cacsilensis*, and a form that falls within the range represented by the rest of nominal subspecies that should be recognized as *L. g. guanicoe* given the taxonomic priority of the latter (Marín, 2004; Marín et al., 2006; Marín et al., in press). Previous molecular studies, on the other hand, using phylogenetic approaches recognized the close relationships between the domestic *Lama glama* ‘llama’ to guanaco (Kadwell et al., 2001), whereas Palma et al. (2001) recovered ‘llamas’ closely related to *L. g. cacsilensis*. The relationship ‘guanaco-llama’ agrees with one of the hypotheses on the origin of domestic forms: that ‘llama’ may have originated from wild populations of guanacos in the Andean puna (Wheeler, 1995). These results also agree with ethnological and archaeological studies conducted by Wheeler (1995) regarding the origin and differentiation of the South American camelids.

It is necessary to clarify the taxonomy of *Lama guanicoe*. This should be done by increasing the number of population samples and combining different approaches, such as molecular, morphometric and modern statistical analyses, as has been done with other South American ungulates, such as the endangered Pampas deer *Ozotoceros bezoarticus* (González et al., 1998; González, Álvarez & Maldonado, 2002). A study that integrates phylogeography along latitudinal and elevational gradients, genetic diversity within and among populations, phenotypic aspects (pelage colouration, body and skull measurements) as well as adaptations to

local habitats, will make an important contribution to understanding the taxonomic status and the evolutionary history of this conspicuous and widely distributed neotropical mammal.

IMPORTANCE FOR GUANACO CONSERVATION

Currently, the 2006 IUCN (The World Conservation Union) Red List of Threatened Species (IUCN, 2006) has given a conservation status for each guanaco subspecies based on Torres's report (1992). Following the latter author, the 2006 IUCN Red List classified each guanaco subspecies mainly based on population size, fragmentation and population trends at a continental level. In South America there are almost 840 000 animals (B. González, unpublished data): over 4000 guanacos assigned to *L. g. cacsilensis* are catalogued as Endangered; *L. g. voglii* contributed with approximately 10 000 animals being classified as Vulnerable with the largest population in northern Argentina; *L. g. huanacus* is classified as Endangered, with less than 3000 animals and finally *L. g. guanacos*, which represents over 97% of the total population, was not classified, being probably out of risk (distribution of each subspecies according to Krumbiegel, 1944).

Guanaco populations have a different conservation status at country level, based mainly on population size without mention of their subspecific classification. Argentina has the largest population ($\approx 91\%$ of total), and therefore the species is classified as either not endangered (Reca, Úbeda & Grigera, 1996) or potentially vulnerable (Díaz & Ojeda, 2000); Chile, on the other hand, classifies the guanaco as Vulnerable ($\approx 9\%$ of the total population) (Glade, 1993). Finally, Bolivia ($< 0.02\%$), Paraguay ($< 0.01\%$) and Peru ($< 0.5\%$) have classified their population as Endangered, following IUCN criteria (IUCN, 1994; Tarifa, 1996).

A clarification and review of the subspecific status of guanacos will be of immense benefit to establish effective conservation from broad to fine scales. Ryder (1986) and O'Brien & Mayr (1991) drew attention to the important role that protection at the subspecific level has in the conservation of biodiversity. Subspecies have the potential to become a new species and are a useful unit for applying legal protection and operational plans. As Torres (1992) claimed: 'South American camelid conservation should be based on knowledge about their taxonomic and systematic position'. Further investigation of the taxonomic status of guanaco populations will give us a robust basis for guanaco classification and guide future conservation management.

Although the subspecific taxonomy approach for making conservation units is criticized by some biologists who stress that it may not be enough to warrant conservation of representative populations (Wikramanayake *et al.*, 1998), we believe that it could be the first step for protecting both ecological functions and evolutionary process where *Lama guanicoe* is present at a broad scale. By applying a hierarchical approach including other relevant information about distributional range, population size and dynamics, genetic distinctiveness to define conservation units, behavioural differences, habitat integrity and quality, and crossed by human pressure, land use, legal protection and administrative limits, we can create an objective-based method for identifying spatial management units that promote total protection, translocations, sustainable use or control at fine scales.

ACKNOWLEDGEMENTS

The authors wish to thank Oscar Skewes and Cristian Bonacic, who helped us to review some specific articles to improve this manuscript. We also thank the comments of Hernán Torres, Domingo Hoces and Erika Cuellar (IUCN/SSC South American Camelids Specialist Group), Simon Milward, Carl Shuster, Ronald Sarno, Jerry Laker and Gabriel Ortega. Special thanks to Fernando Bas and Jane Wheeler. Partial funding from FONDECYT-Chile

(grant No. 1970518 and No. 101105) is greatly appreciated. This article was prepared during the PhD studies of Benito A. González and Beatriz Zapata in the Programa de Doctorado en Ciencias Silvoagropecuarias y Veterinarias of the Universidad de Chile under the support of CONICYT scholarship.

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