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Ecological and biogeographical inferences on two sympatric and enigmatic Andean cat species using genetic identification of faecal samples

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Abstract

The carnivore community of the altiplano ecosystem of the high Andes, including the Andean mountain cat (*Leopardus jacobita*) and pampas cat (*Leopardus colocolo*), is one of the least studied in the world. We determined the origin of 186 carnivore samples (184 faeces and two skulls) collected above 3000 m above sea level in northern Chile, including 33 from the Andean mountain cat and 75 from the pampas cat using diagnostic molecular genetic sequence variation. We determined for the first time food habits, habitat and physiographic associations, and general patterns of molecular genetic variation of the Andean mountain cat and the pampas cat in Chile. Both species had narrow dietary niches dominated by small rodents and there was a wide overlap in diet composition (0.82), suggesting low levels of prey partitioning between species. The mountain viscacha (*Lagidium viscacia*) made up a large proportion of the biomass of the diet of both species, especially for the Andean mountain cat (93.9% vs. 74.8% for the pampas cat), underscoring the importance of further research and conservation focus on this vanishing prey species. Although the probability of finding Andean mountain cat scats increased with altitude and slope, there was substantial geographical overlap in distribution between species, revealing that the pampas cat distribution includes high-altitude grassland habitats. The Andean mountain cat had relatively low levels of mitochondrial DNA (mtDNA) genetic variation (two mtDNA haplotypes) compared with the pampas cat (17 mtDNA haplotypes), suggestive of a distinct evolutionary history and relatively smaller historic populations. These insights will facilitate and provide tools and hypotheses for much-needed research and conservation efforts on these species and this ecosystem.

Keywords: Andean mountain cat, food habits, genetic variation, mountain viscacha, pampas cat

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Introduction

The two cat species most emblematic of the high Andes, the pampas cat (*Leopardus colocolo*) and Andean mountain cat (*Leopardus jacobita*), have been largely unstudied relative to other South American felids (Redford & Eisenberg 1992; Nowell & Jackson 1996). The pampas cat, a small (3–4 kg) cat with a wide range of fur colours, patterns, and coat lengths, has a broad distribution in a variety of grassland habitats from southern Brazil, Peru, Bolivia, Chile and Argentina to the Strait of Magellan, and appears to be more common (García-Perea 1994). By contrast, the Andean mountain cat, a slightly larger species (4–5.5 kg) with grey/brown to a darker reddish/grey fur covered with large dark-red irregular spots and a very characteristic long,

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banded tail, is restricted to the rocky and open, semi-arid and arid treeless areas of over 3000 m above sea level (m a.s.l.) of the altiplano or the high Andes of Argentina, Bolivia, Chile and Peru (Nowell & Jackson 1996; García-Perea 2002; Villalba *et al*. 2004).

From an evolutionary perspective, the Andean mountain cat and the pampas cat are two of seven South American cat species in the ocelot lineage (Johnson *et al*. 2006). Members of this lineage are largely restricted to Central and South America (including Mexico), and based on molecular genetic analyses, began to diverge from a common ancestor around the time period that the land bridge between Central and South America was formed, 2.8 million years ago (Johnson *et al*. 1998, 1999, 2006).

Research on these species in the altiplano has been hampered by numerous factors, including their apparently low local densities, the general inaccessibility of potential study sites, extreme climatic conditions, and a lack of basic information on species distributions, all of which have limited attempts to capture and remotely monitor live animals through radio-telemetry. Both cat species are legally protected in their host countries and by international treaties (Iriarte 1999). The Andean mountain cat is included in the Convention in the International Trade of Endangered Species of Fauna and Flora (Appendix I, CITES 2006) and classified in the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List as 'Endangered with small populations in decline' (IUCN 2006). In contrast, the pampas cat is a CITES Appendix II species (CITES 2006), and in 1996 was removed from the IUCN Red List and reclassified as 'Near Threatened' (IUCN 2006). Similarly, regional conservation assessments have considered these species as 'Endangered' and 'Vulnerable', respectively (Cofré & Marquet 1999). Further, the Andean mountain cat is one of the most threatened and least known felid species in the world (Nowell & Jackson 1996), and as one of the only endemic altiplano species (Redford & Eisenberg 1992; Villalba *et al*. 2004), may be particularly vulnerable to the burgeoning levels of habitat destruction and degradation of Puna ecosystems (Dinerstein *et al*. 1995; Marquet *et al*. 1998; Rundel & Palma 2000). However, information on the presence and abundance of the Andean mountain cat is minimal, consisting primarily of a small number of pelts and skulls in museum collections and a few direct observations reported in the last decade (Osgood 1943; Scrocchi & Halloy 1986; Johnson *et al*. 1998; Iriarte 1999; Sanderson 1999; Delgado *et al*. 2004; Villalba *et al*. 2004).

Because of the paucity of data on Andean mountain cat ecology, numbers, distribution, and evolutionary history, it is difficult to reliably assess its role as one of the primary altiplano predators or its conservation status and vulnerability. Further, a recent compilation of known records for Argentina by Perovic *et al*. (2003) suggests that both cat species overlap in their altitudinal distribution and may be sympatric in some localities. This raises the possibility of interspecific competition. Unfortunately, the distribution, relative abundance, and natural history of the pampas cat are also poorly described, especially in high Andean areas (Nowell & Jackson 1996; Villalba *et al*. 2004).

The purpose of this study was to use molecular genetic analyses of faecal samples combined with ecological and physiographic variables to describe for the first time how the Andean mountain cat and the pampas cat, two small felids with apparently similar phenotypes and natural histories, coexist in the high Andean ecosystem of Chile, by (i) documenting their presence through the genetic identification of their scats, (ii) assessing food habits from faecal analyses of diet and comparing with prey availability, (iii) scrutinizing the genetic diversity of both species in the study area, and (iv) assessing their altitudinal distribution and overlap based on the distribution of their signs (faeces).

Methods

Study area

The study was centred around Salar de Surire Natural Monument (69°04′W 18°84′S) and Las Vicuñas National Reserve (69°19′W 18°56′S) in the Tarapacá Region in northern Chile (First Administrative Region), with some additional samples for dietary analyses collected from other portions of the Antofagasta and Copiapó regions (Second and Third Administrative Regions) of over 3000 m a.s.l. (Fig. 1, Table 1). This region is part of the high-altitude ecosystem or *altiplano*, where the environment is characterized by low atmospheric pressure, high solar radiation, low atmospheric humidity and relatively low and widely oscillating air temperatures (Aceituno 1997). The study area has average monthly temperatures that range between –0.7 and 5.8°C (Luebert & Pliscoff 2006). This is an area with a tropical pluvistational climate regime (Luebert & Pliscoff 2006), with rainfall concentrated in summer (from December to March, 330 mm) due to humidity transport from the eastern slope of the Andes (Garreaud *et al*. 2003; Luebert & Pliscoff 2006). Rainfall decreases towards the southern portions of the study area and temperatures decrease at higher elevations. The vegetation is dominated by low bushes, high grasslands, and cushion plants at high altitudes (Luebert & Pliscoff 2006). In addition, large portions of the region are devoid of any significant plant cover, with extensive areas of exposed sandy or rocky terrain which is often snow or ice covered.

Genetic and phylogenetic analyses

We collected 186 carnivore samples (184 faeces and two skulls) between January and April 2004 (summer) opportunistically

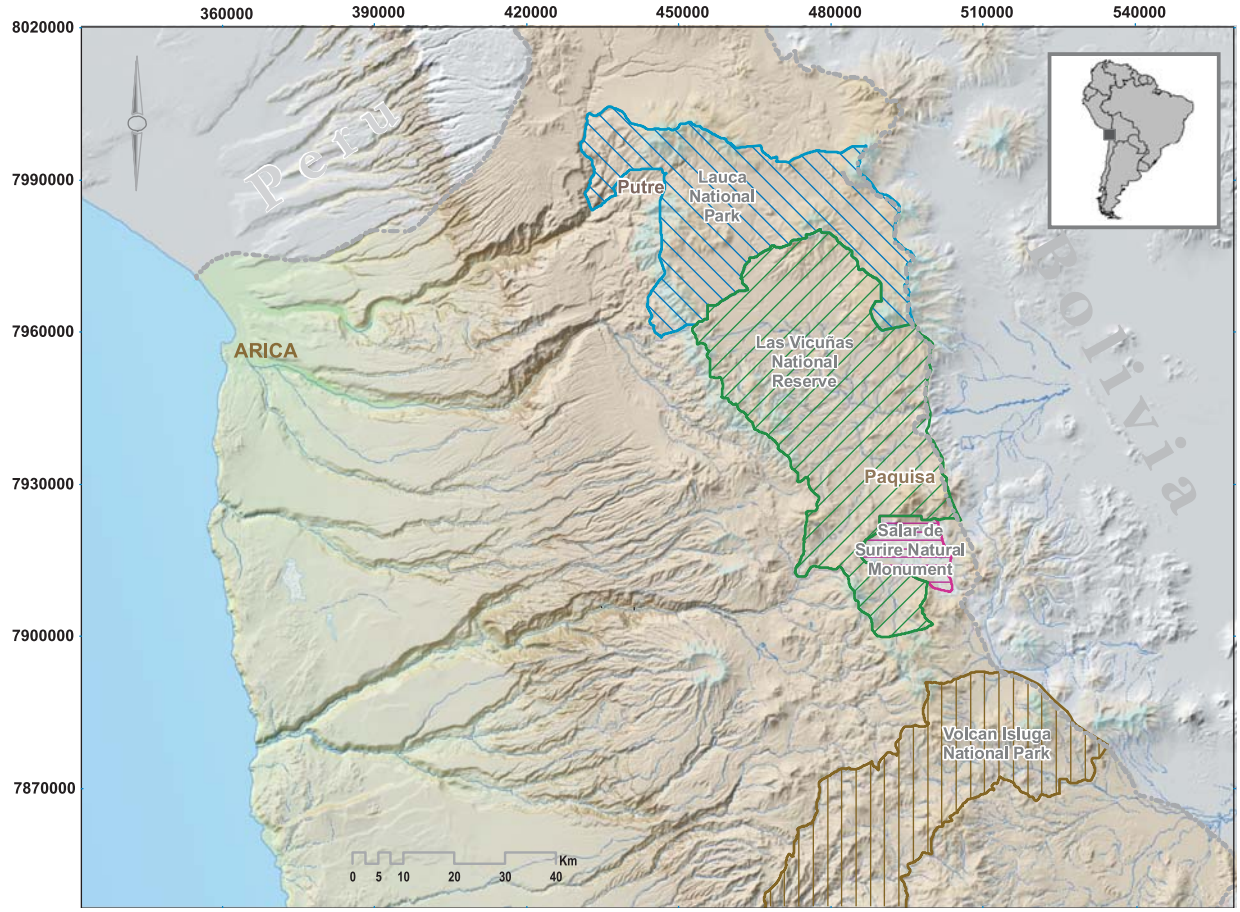

Fig. 1 Map showing location of study area within South America and depicting the main study area centred in Surire Natural Monument and Las Vicuñas National Reserve in the Tarapacá Region in northern Chile. Details are found in Table S1.

Table 1 Summary of samples collected and classified to a species in northern Chile from January to April 2004, total number of samples, number of samples in each altitude range, number of samples in each slope range and number of mtDNA haplotypes (ND felid, nondefined felid; ND haplotype, nondefined haplotype). Details are found in Table S1.

Species	Total no. of samples	No. of samples in each altitude range (*m*)		No. of samples in each slope range (°)		No. of haplotypes
		3200–4000	4001–4600	0–11	12–24	
L. jacobita	33	11	22	12	21	2
L. colocolo	75	47	28	54	21	15
P. concolor	9	0	9	—	—	ND haplotype
C. familiaris	9	6	3	—	—	ND haplotype
ND felid	9	5	4	—	—	ND haplotype
L. culpaeus	8	5	3	—	—	ND haplotype
TOTAL	143					

and through systematic searches, both on and off human and animal trails and relative to geographical features (e.g. along water ways, natural passage ways and below cliffs) in an area of approximately 25 000 ha (Table S1) while doing habitat and small rodent surveys. Faeces that were considered to be from puma or fox (based on size, shape, and high content of insects or seeds) were not collected. When multiple samples were found in latrines, a representative

sample of the freshest scats was collected. Samples were stored in labelled paper bags in a dry place in the field for 1–3 weeks and then at –20 °C in the laboratory to delay DNA degradation (Frantzen *et al*. 1998; Ernest *et al*. 2000; Nsubuga *et al*. 2004). We extracted DNA from the epithelial rectal cells from the outside layer of the faeces and from dried tissue attached to the skulls using a specific kit for faecal material following the manufacturer's suggested protocol (QIAamp DNA Stool Mini Kit). Extractions were performed in a laboratory dedicated to water quality analyses that had not been previously used for genetic research of vertebrates. The species to which the samples belonged was identified by polymerase chain reaction (PCR) amplification using previously published primers and conditions (Johnson *et al*. 1998), sequencing of fragments of ATP-8, 16S, and two portions of NADH-5 mitochondrial DNA (mtDNA) genes and comparing these against reference sequences (Johnson *et al*. 1998). PCR amplifications were repeated at least twice for each gene fragment (342 bp of 16S, 147 bp of Atp-8, 280 bp of ND5 mtDNA genes) to ensure repeatability of species identification and haplotype assignment. Only samples for which complete sequences from at least two genes fragments were sequenced successfully were assigned to a species, and haplotypes were assigned only for samples sequenced at least twice for all three gene segments.

Phylogenetic relationships among mtDNA haplotypes were assessed using three approaches implemented in PAUP* (Swofford 2001). A maximum-parsimony (MP) analysis was conducted using a heuristic search, with random addition of taxa and tree-bisection–reconnection branch swapping. The minimum evolution (ME) heuristic search approach consisted of neighbour-joining trees constructed from Kimura 2-parameter distances followed by a branch-swapping procedure. Maximum-likelihood (ML) analysis was done using the parameters as estimated by MODELTEST 3.06 (Posada & Crandall 1998). The reliability of the nodes in each of the analyses was assessed by 100 bootstrap iterations. Measures of population genetic variation such as mean number of pairwise differences, gene diversity and nucleotide diversity were estimated using ARLEQUIN 2.0 (Schneider *et al*. 2000).

Food habit analysis

Only faeces identified molecularly were analysed for food habits. Undigested remains in faeces were separated through a binocular microscope. Contents were identified to the finest taxonomic level possible based on available literature and comparison with a voucher collection. Mammal remains were identified using teeth keys (Reise 1973; Pearson 1995; Steppan 1995) and skeletal remains, while birds were identified from the shape and size of the nodules in feather barbules (Reyes 1992; Rau & Martínez 2004).

We estimated the percent frequency of occurrence of prey items in the diet of each species for the calculation of niche breadth and overlap. We estimated the relative biomass consumed for each prey item (% B_i), a measure of the importance of each prey item, as in Rau (2000) where B_i (%) = 100 ($n_i\ m_i/\Sigma n_i\ m_i$) and n_i is the minimum relative number of prey items and m_i is the average body mass of prey item. The mean weight of each vertebrate prey species was calculated from field data and from literature (Jaksic *et al*. 1983; Redford & Eisenberg 1992; Muñoz-Pedreros 2000). Because adult mean weights were used in these calculations, the results may overestimate the biomass in the diets. Presumed temporal and spatial activity patterns of rodents were obtained from Redford & Eisenberg (1992) and Muñoz-Pedreros (2000).

To evaluate trophic niche breadth, we used the Levins (1968) index: $B = 1/(\Sigma p_i^2)$ where p_i is the relative frequency with which a species uses the i resources. A standardized index of trophic niche breadth (Colwell & Futuyma 1971) was calculated as follows: $B_{sta} = (B - B_{min})/(B_{max} - B_{min})$, where B is Levins index of niche breadth, B_{max} is the total number of food categories and B_{min} is the minimum niche breadth possible. B_{sta} values can range between 0 (minimum niche breadth) and 1 (maximum niche breadth). Trophic niche overlap was computed using the Pianka (1973) index: $O_{jk} = \Sigma p_{ij}\, p_{ik}/(\Sigma p_{ij}^2\, \Sigma p_{ik})^{1/2}$ where p is the proportion of food category i in species j and k. Values of niche overlap range from 0 (no overlap) to 1 (complete overlap).

The relative abundance of small mammals in the study area was determined by capture–recapture methods using Sherman traps (23 cm × 9 cm × 7.5 cm) placed in two grids of 49 traps each, 10 m apart, covering an area of 0.64 ha (70 × 70 m, plus an influence area of 5 m). Traps were set in shrubland *(Parastrephia* spp.*)* and grassland *(Festuca* spp.*)* habitats for three consecutive nights. Trapping was carried out during the same period as the faeces collection, January–April 2004. Traps were checked and rebaited with crushed oats twice a day, at dawn and dusk. We used capture–mark–recapture methods, marking the captured rodents by cutting specific dorsal hair. Captured rodents were identified, weighed and measured (total length, tail length, tarsum length, ear length) (data not shown) and then released in the same places they were captured. Data was analysed independently for both dawn and evening trapping sessions and calculations were made considering 5 sessions (the first was not used since there were no recaptures). The relative abundance of small mammals was estimated by the Schnabel index (Krebs 1989): $N = \Sigma(A_t\ B_t)/\Sigma(C_t)$ where N = total population, A_t = total number of captured individuals in the sample t, B_t = number of marked individuals before the sample t, C_t = number of previously marked individuals in the sample t.

The frequency of appearance of the prey items in the diet of both felids was compared with the frequency the prey

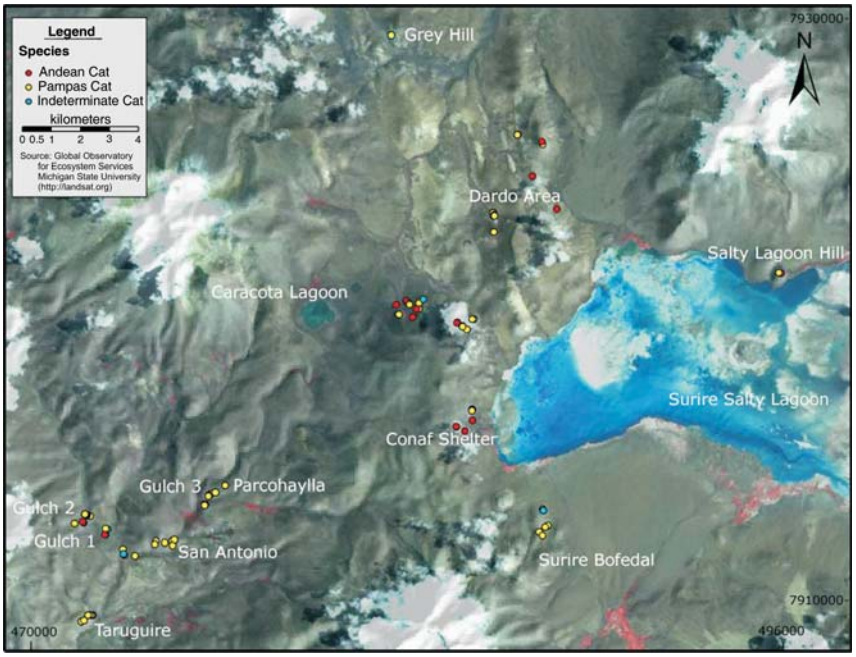

Fig. 2 Sites of Andean mountain cat and pampas cat faecal samples portrayed on Landsat 7 ETM satellite image of the core study area, near Surire Salty Lagoon in the Tarapacá Region. Landmarks and locations noted in Table 1 are labelled.

items occurred in the trapping survey to determine whether the felids fed on their prey in the same proportion as they appeared in the field using the Manly Chesson preference index (Chesson 1983). Unidentified items and plants were excluded from these comparisons.

Spatial distribution

To assess the spatial distribution of both species in the study area and their overlap, we characterized the location where scats were collected with regards to: (i) topography (altitude and slope), and (ii) distance to nearest vegetated area, water sources, roads and villages. Topographic variables, altitude and slope, were obtained from the digital elevation models obtained from the Shuttle Radar Topography Mission (SRTM), at a resolution of 90 m. Vegetation was obtained from the analysis of Landsat 7 ETM+ satellite image with resolution of 28.5 m. We identified areas covered by vegetation using the normalized difference vegetation index (NDVI) with the near infra-red (band 4) and the red (band 3) spectral bands employing the following formula NDVI = [(band 4 – band 3)/(band 4 + band 3)]. NDVI varies from –1 to +1, and values greater than 0.1 suggest the presence of vegetative cover (Chuvieco 2002). We calculated the distance of each scat to a pixel with NDVI > 0.1 as an estimate of the distance to the nearest area with vegetation. The distance of each sample to water features, roads, and villages were estimated from information layers (1:50 000) from the Chilean Geographic Military Institute. All digital information was incorporated into a Geographical Information System (ArcGIS 9.1 with Spatial Analysis extension and ERDAS 8.5) with the coordinate system UTM zone 19 south datum WGS 84.

To assess what factors affect the presence of both species, we assessed how geographical factors correlated with the presence of their signs (faeces) by building a generalized linear model with a binomial error distribution (i.e. logistic regression). The presence/absence records of each cat species was used as the response variable, while the predictor variables were altitude, slope, distance to human settlements, distance to water, and NDVI. To find the best model we used a step-wise procedure and the Akaike information criteria (see Harrell 2001). Model significance was assessed using a maximum likelihood test with a chi-square approximation (Dalgaard 2002). Models were fitted using the R package (R Development Core Team 2005).

Results

Of the 186 samples collected (184 scats and two skulls), PCR products were successfully amplified and sequenced from 143 (76.8%). With these sequences, 75 samples were identified as pampas cat, 33 as Andean mountain cat, nine as domestic dog (*Canis familiaris*), nine as puma (*Puma concolor*), eight as culpeo fox (*Lycalopex culpaeus*), and nine (from faecal samples) were categorized as an unidentified cat species due to ambiguous sequences (Table 1, Fig. 2). The scats from Andean mountain cats and pampas cats were found primarily within or near caves in rocky formations. As has been observed for the Geoffroy's cat (*Leopardus geoffroyi*) and kodkod (*Leopardus guigna*) (Johnson & Franklin 1991), scats were often found in latrines with numerous faeces of different

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          111111 1112223333 3333334444 4444444444 5555555555 5555555555 5566666666 6666667777 7777
       2567112225 6680331256 6689990022 2444557789 0000111233 3344456678 8800122345 6777891222 3344
       6299256796 1275363173 7840793957 9478351358 3689256103 4905973790 1749406659 5267667236 0606
Lco258 TTATCACCCT CCTTACTCCT ATGCTCTGAA GTATGTTGCT TTCCCACTTT TCTCAACCAG TTCGCCTAAT AGTCCCTATA TTTC
Lco044 .......... .......... .......... .......... .......... .......... ...A...... .......... ....
Lco149 .......... .....T.... .......... .C........ .......... .......... .......... .......... ..C.
Lco194 .......... .....T.... .......... .C........ .......... ......T... .......... .......... ..CT
Lco196 .......... .....T.... .......... .C........ .......... ......T... ...A...... .......... ..CT
Lco263 ........T. .........C .......... .C......T. .......... .......... .......... .......... ....
Lco161 .....G.... .........C G..T....G. ........T. .........C .......... ...A...... .......... ....
Lco251 .....G.... .......... .......... .......... .........C .......... .......... .......... ....
Lco186 .....G.... .......... .......... .......... .........C .......... ...A...... .......... ....
Lco183 .....G.... .......... ........G. ........T. .........C .......... .......... ......G... G...
Lco239 ........T. .........C .......... .C......T. .........C ...G.G.... .......... .......... ....
Lco198 ........T. .........C .......... .C......T. ......T... .......... .......... .......... ....
Lco076 ........T. .......T.C .......... .C......T. ......T... .......... .......... .......... G...
Lco271 ........T. .........C .......... .C......T. ......T... .......... .......... ......G... ....
Lco105 ........T. .........C .......... .C......T. ......T... .......... ...A...... .......... ....
Lco026 ........T. .........C .......... .C......T. ......T... .......... .......... .......... GG..
Lco184 ........T. .........C .......... .C......T. ......T... .......... ...A...... .......... GG..
Lco-7  .........C ....G....C .......... .......... .......... .........A ...A...... ..C.T.C... ....
Lco-11 .C.......C .........C ....C..... ........T. .......... .........A ...A..C... ..C.T.C... ....
Lco-29 .C.......C .........C .....T.... ........T. .......... ....G....A ...A...... ..C.T.C... ..C.
Lco-10 .C........ .........C .....T.... ........TC .....G.... ....G..... ...A...... .A........ ....
Lco-12 .C........ .........C .......... ........TC .....G.... ....G..... ...A...... .A.T...... ....
Lco-23 .......... .........C ...TC..... ........TC ....T.T... .......... ...A...... .......... ....
Lco-26 .......... .........C ...T...... ........TC ....T.T... .......... ...A...... ......C... ....
Lco-9  .......T.. .........C ...T...... ........TC ........CC .......... ...A.T.... .......... ....
lti-31 .......T.. ...C.....C ...T...... ........TC ........CC .......... ...A...... .......... ....
lti-32 .......T.. ...C.....C ...T...... ........T. ..TG....CC .......... ...A...... .......... ....
lti-36 .......T.. ...C..C..C ...T...... ........TC ........CC .......... ...A...... .......... ....
Lja1   C..CT.T..C AT.C...TT. .CAT..CA.C A.GCACCAAC CC.A...... CTC...ATGA CCTAT..GGC G....TCGCG ....
Lja2   C..CT.T..C AT.C...TT. .CAT..CA.C A.GCACCAAC CC.A...... CTC...ATG. CCTAT..GGC G....TCGCG ....
Oja04  C...T.T..C AT.C...TT. .CAT..CA.C A.GCACCAAC CC.A...C.. CTC...ATGA CCTAT..GGC G....TCGCG ....
Oja84  C...T.T..C ATCC...TT. .CAT..CA.C A.GCACCAAC CC.A...C.. CTC...ATGA CC.AT..GGC G....TCGCG ....
Oja03  C.G.T.T..C ATCC...TT. .CAT..CA.C A.GCACCAAC CC.A...C.. CTC...ATGA CC.AT..GGC G....TCGCG ....
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Fig. 3 Variable sites defining Andean mountain cat and pampas cat mtDNA haplotypes in northern Chile.

ages. The relatively lower numbers of puma and fox faeces does not necessarily reflect relative densities, as faeces presumed to be from these species were not collected.

Genetic variation

Complete sequences (342 bp of 16S, 147 bp of Atp-8, 280 bp of ND5 mtDNA genes) were obtained from 78 scats and were used in analyses of molecular genetic variation. From these 769 bp, 21 fixed diagnostic sites distinguished Andean mountain cat sequences from pampas cat sequences (four 16S, six Atp-8, and 11 ND5 sites), and were used to identify 27 Andean mountain cat scats and 51 pampas cat scats (Table 1). An additional six samples of Andean mountain cats and 24 pampas cat samples were identified from partial sequences using between three and 10 unambiguous diagnostic sites. The 27 complete Andean mountain cat sequences (769 bp) defined two haplotypes, Lja-1 from 22 scats and Lja-2 from five scats. Only one variable site distinguished these two haplotypes. Lja-1 was distributed throughout the study area, but four of the five Lja-2 haplotypes were clustered together in the northern portion of the study area. The two Andean mountain cat haplotypes most closely resembled the previously described Oja-04 haplotype from a museum sample collected in the Third Region of Chile (Johnson *et al*. 1998) (Figs 3 and 4).

The 51 pampas cat scats defined 17 pampas cat haplotypes (Table 1, Fig. 3). Lco-263, found in eight samples, was the most common, followed by Lco-186 and Lco-198, which were found in six samples each. Twenty-one variable sites were found among these haplotypes, which differed by one to 13 sites and for which there was a mean of 6.5 steps among the haplotypes. There was modest support based on a maximum likelihood, maximum parsimony, and minimum evolution phylogenetic analyses that 16 of these 17 haplotypes were most closely related to samples from the central Chilean Andes and western Argentina (Lco-7, Lco-11, and Lco29) (Fig. 4). However, haplotype Lco161, found in one individual was closely related with haplotypes Lco-13 and Lco-28 found in individuals in Brazil.

Food habits

Faeces of Andean mountain cat and pampas cat, based on the genetic analyses (Table 1), were analysed to assess food habits of both small felids. Our findings suggest that the main component of the diet of both pampas cat and Andean mountain cat was rodents (71% and 82%, respectively),

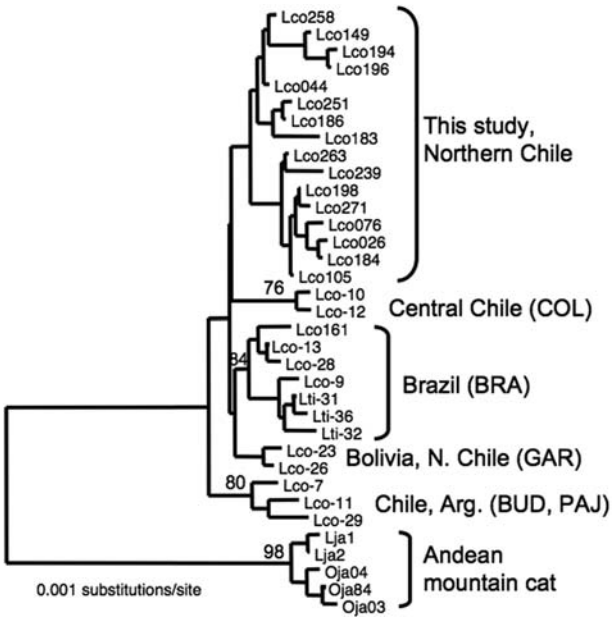

Fig. 4 Phylogenetic relationships of Andean mountain cat and pampas cat mtDNA haplotypes depicted on a maximum-likelihood tree. Nodes with bootstrap support values for the minimum evolution, maximum parsimony, and maximum-likelihood analyses of greater than 50% are noted with their maximum-likelihood value. Andean mountain cat haplotypes Lja1 and Lja2 are from this study and Oja haplotypes are from Johnson *et al*. (1998). Pampas cat haplotypes are labelled by their general geographical origin and subspecies designation as follows: COL for *L. c. colocolo*; PAJ for *L. c. pajeros*; GAR for *L. c. garleppi*; BRA for *L. c. braccatus*; and BUD for *L. c. budini*.

followed by birds (27.5% and 18%) (Table 2). For pampas cats, 23% of the birds corresponded to one of three species of flamingos (Phoenicopteriformes) and 4.5% to tinamous (Tinamiformes). All of birds in the Andean mountain cat scats were tinamous (Tinamiformes). Flamingo feathers found in pampas cat faeces were pink, and not brown or grey as from young flamingos, suggesting they belonged to adults. The trophic niche of the pampas cat was wider (B_{sta} = 0.349) than the Andean mountain cat (B_{sta} = 0.249). The Andean mountain cat can be characterized as a specialist, preying mostly on the mountain viscacha, while the pampas cat is more of a generalist species, preying on a larger variety of rodents and birds. This feeding characterization is consistent with the broader geographical distribution of the pampas cat. Food niche overlap between the two cats was extensive (0.82), indicative of low prey partitioning.

Cursorial-nocturnal rodents occurred in 37% of pampas cat and 33.9% of Andean mountain cat scats, respectively, compared with 33% and 48.1% for cursorial-diurnal rodents and 1% and 0% for fossorial-diurnal rodents, respectively. The most common prey species of pampas cat were species of leaf-eared mice (*Phyllotis* spp.) (found in 31.5% of scats), a cursorial–nocturnal rodent and the mountain viscacha (*Lagidium viscacia*) (29%), a cursorial–diurnal (sometimes also described as crepuscular) rodent generally found in colonies, which can be quite large. Similarly, but in reverse order, the most common prey items of the Andean mountain cat were mountain viscacha (44.1%) and leaf-eared mice (27.6%). For both cats, viscacha was the most important prey item based on relative biomass (74.8% for pampas cat and 93.9% for Andean mountain cat; Table 2). Vegetable matter was found only occasionally in scats and was not included in the analyses.

The rodent with the highest relative density in both habitats was the white-bellied field mouse (*Akodon albiventer*) (3.39 ha^{-1} and 7.89 ha^{-1} for shrubland and grassland, respectively), followed by leaf-eared mice (*Phyllotis* spp.) (1.17 ha^{-1} and 7.53 ha^{-1} for shrubland and grassland, respectively) and the Andean field mouse (*Abrothrix andinus*) (1.17 ha^{-1} and 3.52 ha^{-1} for shrubland and grassland, respectively). Shrub habitat had a considerably lower density of rodents (5.73 ha^{-1}) than grassland habitat (18.94 ha^{-1}). We compared the relative frequency of small rodents in the diet of both felids with the relative frequency in which these prey items occurred in the trapping survey to determine whether these felids fed on small rodents in the same proportion as they appeared in the field. According to the Manly Chesson preference index, both felids fed on the diurnal field mice (the 30 g *A. albiventer* and 31 g *A. andinus*) less than predicted by their abundance in the field and showed evidence of selection for the larger and more nocturnal leaf-eared mice (48 g). These results show that both felids preyed on both diurnal/crepuscular species like the viscacha, as well as more nocturnal prey such as the leaf-eared mice.

We analysed several faecal samples from five latrines as a preliminary assessment of whether latrines were used by multiple species. Four of these latrines had only Pampas cat scats while the fifth was faeces from both culpeo fox and domestic dog.

Distribution modelling

The best logistic models for predicting the presence or absence of Andean mountain cat and pampas cat scats were determined using altitude, slope, distance to human settlements, distance to water, and distance to vegetation were used as predictor variables. Within the core study area (around Surire Natural Monument and Las Vicuñas National Reserve), 32 out of the 106 sites were assigned to *Leopardus jacobita* and 54 to *Leopardus colocolo* (scats from other species were found at the other 20 sites). Distance to water and distance to vegetation were not informative and were not included in the models. The best model to predict the probability of occurrence was similar for both species (Table 3, Fig. 5). For pampas cat, the model included altitude and slope, and for Andean mountain cat it included altitude,

Table 2 Summary of prey species identified in *Leopardus colocolo* and *Leopardus jacobita* faecal samples, including adult body mass and behaviour and activity patterns. Contribution to the diet is estimated by the number of times prey item appeared in scats, the percent contribution of these prey items relative to the total number, the number of scats containing each item and the estimated relative percent biomass prey items contributed to the total diet (Curs, cursorial; Foss, fossorial; Noct, nocturnal; Diur, diurnal; Crep, crepuscular)

				L. colocolo				*L. jacobita*			
Prey species	Average adult body mass (g)	Primary lifestyle	Activity patterns	No. of prey items	Percentage of items	No. of scat item found	Percentage biomass	No. of prey items	Percentage of items	No. of scat item found	Percentage biomass
Rodents											
Andean field mouse (*Abrothrix andinus*)	31	Curs	Diur	4	2	1	0.1	0	0	0	0
Leaf-eared mice (*Phyllotis* spp.)	48	Curs	Noct	63	31.5	17	1.7	35	27.6	11	1.7
White-bellied field mouse (*Akodon albiventer*)	30	Curs	Diur	4	2	2	0.1	5	4	3	0.3
Highland desert mouse (*Eligmodontia puerulus*)	20	Curs	Noct	9	4.5	5	0.2	0	0	0	0
Tuco-tuco (*Ctenomys opimus*)	200	Foss	Diur	2	1	2	0.8	0	0.0	0	0
Mountain viscacha (*Lagidium viscacia*)	1600	Curs	Crep	58	29	23	74.8	56	44.1	18	93.9
Chinchilla rat (*Abrocoma cinerea*)	250	Curs	Noct	2	1	2	1	8	6.3	3	2.5
Total rodents				142	71		78.7	104	82		98.4
Birds											
Flamingo species (*Phoenicopteridae*)	4500			46	23	2	18.3	0	0	0	0
Tinamou species (*Tinamiformidae*)	250			9	4.5	6	3	23	18	2	1.6
Total birds				55	27.5		21.3	23	18		1.6
Insects				3	1.5	2	0	0	0.0	0	0
Total				200				127			

	Estimate	Standard error	*z* value	Pr(> |z|)
Andean mountain cat				
Intercept	–10.470000	4.0210	–2.600	0.009
Altitude	0.002304	0.0011	2.170	0.029
Slope	0.040250	0.0198	2.030	0.041
Distance to human dwellings	–0.000369	0.0002	–1.800	0.070
Null deviance: 123.81				
Residual deviance: 110.48				
Likelihood test chi square: 0.004				
Pampas cat				
Intercept	8.887265	3.7988	2.339	0.019
Altitude	–0.002020	0.0010	–1.996	0.045
Slope	–0.032005	0.0189	–1.691	0.090
Distance to human dwellings	0.000276	0.0002	1.389	0.164
Null deviance: 132.53				
Residual deviance: 121.98				
Likelihood test chi-squared: 0.014				

Table 3 Variables (coefficients, standard error and *P* values) describing the best logistical models for Andean mountain cat and pampas cat scats based on altitude, slope, and distance to human settlements (DHS)

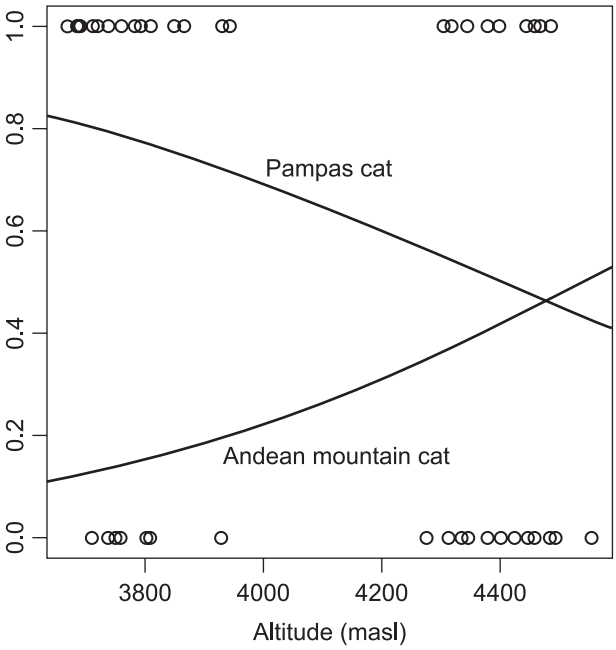

Fig. 5 Plot depicting the probability of finding an Andean mountain cat or pampas cat scat relative to altitude in northern Chile.

slope, and to a lesser extent distance to nearest human settlements. Although signs of both species were found essentially through the same altitudinal ranges in the study area (from 3714 to 4494 m a.s.l. for Andean mountain cat and from 3670 to 4487 m a.s.l. for pampas cat), the probability of finding pampas cat decreased with altitude, while the opposite trend was observed for the Andean mountain cat (Table 3, Fig. 5). A similar relationship was observed for the variable slope, for which the Andean mountain cat showed a positive response while the opposite was observed for the pampas cat. The average slope for the sites of Andean mountain cat scats was 13° compared with 10° for pampas cat. The best model for the Andean mountain cat also included a negative effect for distance to human settlements.

Population size estimates

An estimate of the number of individuals sampled in our 25 000 ha core study area can be assessed in several ways. Using the formula proposed by Scrocchi & Halloy (1986) for estimating the carrying capacity of the altiplano habitat for Andean mountain cats (0.6 kg/km^2) and a conservative body mass of 5 kg, 30 individuals could theoretically inhabit the core study area. Alternatively, using the estimated home range size of an Andean mountain cat in the Bolivian altiplano of 47.12 km^2 (Villalba, unpublished), approximately five to 10 Andean mountain cats would inhabit the core study area, assuming either no range overlap or a conservative average of two animals per home range, as would be more common for felids (Redford & Eisenberg 1992; Nowell & Jackson 1996; Sanderson *et al*. 2002).

More directly, we can estimate the number of animals sampled based on the occurrence of different haplotypes. Minimally the two sampled mitochondrial haplotypes represent two individuals in the core study area. However, if we assume that any pair of samples with the same haplotype, but farther than 20 linear km from each other, represent different individuals (based on the theoretical densities and home range sizes discussed above), at least three different Andean cat individuals had haplotype Lja-1 and at least two individuals had haplotype Lja-2, for a total of five individuals.

For the pampas cat, Quintana *et al*. (2000) estimated there were 0.9 individuals per 1000 ha in the Argentinean Patagonia, which would correspond to 22 pampas cats in the 25 000-ha core study area. Using estimates of home range sizes of 39.80 km^2 based on tracking analysis in the Bolivian altiplano (Villalba, unpublished), this would translate to approximately six to 12 individuals (assuming the same amounts of range overlap discussed above). However, more directly, within the core study area 14 haplotypes were represented, which would correspond to at least 15 individuals assuming samples with identical haplotypes that were found farther than 20 km apart represent two individuals.

Extending this logic to areas outside the core study site, a minimum of six additional pampas cat individuals (21 total) are represented by our scat data.

Discussion

Genetic inferences

Our results provide additional evidence that the Andean mountain cat is a relatively rare species with unique ecological and genetic characteristics. Even in what might be prime Andean mountain cat habitat in our core study area, almost twice as many locations with pampas cats scats were identified compared with the Andean mountain cat (51–27), which based on the distribution of unique haplotypes corresponded to five Andean mountain cats and 15 pampas cats. Although the markedly lower number of mitochondrial DNA haplotypes observed in the Andean mountain cat could have resulted from behavioural differences between the two species, more likely the genetic variation reflects a smaller current or historic population size and a more recent coalescence date relative to the pampas cat. These two Andean mountain cat haplotypes are very similar to previously described haplotypes obtained primarily from museum samples (Johnson *et al*. 1998). Whether this lack of genetic diversity is masking significant population structure will require broader geographical sampling and additional molecular studies.

The pampas cat mitochondrial DNA haplotypes identified in this study formed a group of related haplotypes. They showed some affinity, but no significant grouping, with previously described haplotypes found in voucher specimens from several pampas cat subspecies in neighbouring parts of South America. These included Lco-7, Lco-11, and Lco-29 from the central Chilean Andes and western Argentina (*L. c. colocolo* and *L. c. pajeros*), Lco-10 and –12 from the central Chilean coastal mountains (*L. c. colocolo*), and Lco-23, –26 from Bolivia (*L. c. garleppi*) (Fig. 4). The one exception was haplotype Lco-161, which is very similar to southern Brazilian haplotypes. These results call attention to the need for additional molecular genetic studies on the pampas cat using a broader range of autosomal markers. However, the results provide strong evidence that pampas cat populations retain large amounts of genetic variation and in the Chilean altiplano have maintained relatively high population sizes and have not experienced recent demographic bottlenecks. The lack of shared haplotypes in northern Chile with the small sample of animals from neighbouring geographical areas is evidence that these areas are possibly genetically structured and that they may have experienced significant and lengthy periods of isolation and reduced gene flow.

Ecological inferences

The altiplano of the high Andes is home to a unique assemblage of carnivore species. Some of these, such as the culpeo fox, the puma and the pampas cat are generalist with wide geographical distributions through several biogeographical zones and habitats (Rau *et al*. 1991; Redford & Eisenberg 1992; Nowell & Jackson 1996; Quintana *et al*. 2000), while others, because of their more restricted distribution, appear to be more specialized and perhaps more specifically adapted to this high-altitude arid habitat. The Andean mountain cat is a good example of this phenomenon, where this species is seemingly limited, for currently unknown reasons, to high Andean habitats (Redford & Eisenberg 1992; Nowell & Jackson 1996; Yensen & Seymour 2000).

The coexistence of sympatric carnivores of similar size, morphologies, and food habits is generally facilitated by differential resource use (Farrell *et al*. 2000). Prior to the start of this study, it was commonly presumed that Andean mountain cats and pampas cats would segregate into fairly disjunct distributions, with relatively little local overlap in contact zones that they might co-inhabit (but see Perovic *et al*. 2003). Because the pampas cat is found throughout much of the relatively open, grassy regions of central and southern South America, while the Andean mountain cat was found only at altitudes of more than 3000 m a.s.l., it was assumed that coexistence would most likely be a function of altitude, and less likely a function of habitat, behaviour, or prey availability.

However, the distribution of scat samples in our core study area in northern Chile suggests substantial overlap in distribution is possible and that local resource partitioning based on differential habitat and prey utilization is likely. As expected, the probability of encountering an Andean mountain cat instead of a pampas cat scat increased with altitude. However, this variable alone was unable to explain distribution patterns, as the range of altitudes overlapped considerably (Table 1) and scats were often located in fairly close proximity. Because our data are based on the spatial location of faecal samples instead of sightings or telemetry readings, and is thus associated with a single behaviour (defecating), it might be somewhat deceptive. However, since the locations where faeces were collected appear to be used continuously, we believe that they provide a suitable

first approximation for the spatial distribution of each species within the study area.

Our data, based on where scats were located and what species they contained, provide some evidence for behavioural differences between the two cat species. Although both preyed upon the same species and had a high degree of prey overlap (82%), pampas cats fed more frequently on birds (especially Flamingo species) and small rodents and relied much less in terms of percent biomass consumed, on the mountain viscacha. Extrapolating from what is known about the behaviour and ecology of the these prey species, pampas cats spend more time foraging in the flatter, more open wetlands (bofedales) and grasslands on waterfowl like flamingos and on smaller, cursorial rodents, while the Andean mountain cats spend more time in the steeper, rocky areas frequented by the mountain viscacha. However, both cat species seem to have similar activity patterns, since their diets include both nocturnal and diurnal small, cursorial rodent species and both feed heavily on the diurnal/crepuscular mountain viscacha.

The preponderance of the mountain viscacha in the diet of both cat species, combined with similar findings in Argentina (Walker *et al*. 2007), underscores the potentially ecological importance of viscacha populations. The mountain viscacha, one of several similar species found in the South American Andes, is classified as 'vulnerable' in Chile (CONAF 1993). It inhabits the rocky, sparsely vegetated habitats of the Andean highlands between the tree line and the snow line (3000–5000 m a.s.l.) where it feeds on a wide range of plants (Marquet *et al*. 1998; Cortés *et al*. 2002). They live in family groups that can number in the hundreds and generally do not move far from natural cavities between rocks, which they use as shelter and refuge as they are very poor diggers (Ziesler 1992; Galende *et al*. 1998; Sanderson 1999). Viscacha populations are vulnerable to exploitation by humans (for fur and meat) because of their low reproductive rate of one or two young per year, their trophic specialization, sedentary behaviour and sensitivity to habitat degradation resulting from human activities such as the desertification of altiplano wetlands from mining operations (Galende *et al*. 1998). Although humans also pose a threat to small cats like the Andean mountain cat and pampas cat, improving the long-term prospects of these predators might depend heavily on maintaining and extending the range and number of viscacha colonies, which historically have been destroyed or severely reduced. This species might also serve as an important indicator for identifying areas possibly inhabited by Andean mountain cats and Pampas cats.

In summary, based on the spatial distribution of scat locations and the analyses of their prey contents, we hypothesize that the pampas cats, and to a lesser extent the Andean mountain cats, have flexible, opportunistic hunting strategies and that both have similar, crepuscular or generally flexible activity patterns, as has been documented in other South American small cat species like the Geoffroy's cat (Johnson & Franklin 1991). The main ecological differentiation among these species in areas of sympatry seems to be in their use of habitat because pampas cats spend more time foraging in the flatter, more open wetlands and grasslands, and less time in the steeper, rocky areas frequented by the mountain viscacha as extrapolated from the behaviour and ecology of their prey species. Also, coexistence between the Andean mountain cat and pampas cat could be facilitated by concentrations of locally abundant prey species such as the mountain viscacha and flamingos (Sunquist & Sunquist 1996). The spatial overlap may also be dictated in part by factors that we were unable to address in this study such as home range and movement patterns relative to available vegetative cover or rocky outcrops and cliffs used for diurnal resting and denning sites, movements relative to local densities of available prey, and population density (Johnson *et al*. 1996).

Further studies, including live capture and detailed radiotelemetry monitoring in a variety of habitats and additional molecular genetic surveys are needed to test these preliminary observations of partial spatial segregation between species. It is especially urgent to obtain a fuller, more detailed understanding of basic life history and ecological characteristics, as well as more precise density estimates of the Andean mountain cat. This is probably the more vulnerable of the two species as it apparently exists at very low population densities, preys extensively on a vanishing prey species, and is one of the few felid species for which there are no records of animals being held in captivity (Iriarte 1999).

Combining molecular genetic data with additional data from faecal samples has proven to be a particularly effective way to obtain important information on elusive, difficult to study species. As employed in our study, this strategy has provided unique insights into the ecology and population genetics of the enigmatic Andean mountain cat and pampas cat, and has provided some of the first data sets through which crucial field studies and conservation actions can be designed and implemented.

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Supplementary material

The following supplementary material is available for this article:

Table S1 Location of samples collected in northern Chile from January to April 2004, including physical description of habitat and vegetation, species identification based on diagnostic mtDNA variation, and mtDNA haplotype

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-294X.2007.03606.x
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