Journal of Mammalogy, xx(x):1–9, 00
DOI:10.1093/jmammal/gyy065

External and skull morphology of the Andean cat and Pampas cat: new data from the high Andes of Argentina

Cintia Gisele Tellaeche,* Juan Ignacio Reppucci, Miriam Mariana Morales, Estela Maris Luengos Vidal, and Mauro Lucherini

Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy, Consejo Nacional de Investigaciones Científicas y Técnicas, Jujuy, Argentina (CGT, MMM)
CETAS - Centro de Estudios Territoriales Ambientales y Sociales, Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy, Alberdi 47, Jujuy, Argentina (CGT, MMM)
APN-DRNOA (Delegación Regional Noroeste, Administración de Parques Nacionales), Consejo Nacional de Investigaciones Científicas y Técnicas, Santa Fe 23, Salta, Argentina (JIR)
GECM–Mammal Behavioural Ecology Group, Laboratorio de Fisiología Animal, Instituto de Ciencias Biológicas y Biomédicas del Sur (INBIOSUR), Departamento de Biología Bioquímica y Farmacia, Universidad Nacional del Sur (UNS)-CONICET, Bahía Blanca, Argentina (EMLV, ML)

* *Correspondent: cintiatellaeche@gmail.com*

Andean and Pampas cats are 2 Neotropical small felids of the genus *Leopardus*. Until now, most of the scarce morphometric data published for these felids, especially the rare Andean cat (*L. jacobita*), were obtained from museum skins and skulls of undetermined sex. Here, we present morphological data from Pampas cats (*L. colocolo*) and the largest sample of live Andean cats (5 Andean cats and 6 Pampas cats) captured in the Argentine High Andes. We provide a craniometric analysis of all available adult skulls of Andean cats, including the first known female specimens of Andean and Pampas cats ($n = 42$). We nearly double the number of published external measurements for live Andean cats, and provide measurements and photos of all available skulls of adult Andean cats, including 2 new skulls with known sex. The data show that Andean cats are larger than Pampas cats and morphometric differences may be related to sexual dimorphism in both species. Principal component analysis of skull measurements showed almost complete separation of Andean and Pampas cats.

El Gato Andino y el Gato del Pajonal son 2 félidos Neotropicales de pequeño tamaño pertenecientes al género *Leopardus*. Hasta el momento la mayoría de la escasa información morfométrica publicada acerca de estos 2 félidos, especialmente del Gato Andino, fue obtenida de pieles de museo y cráneos, en su mayoría sin sexo conocido. En este trabajo presentamos datos morfométricos de la muestra más grande de animales vivos nunca antes estudiada de Gato Andino y Gato del Pajonal (5 Gatos Andinos y 6 Gatos del Pajonal) capturados en los altos Andes de Argentina y un análisis craneométrico de los 6 cráneos de especímenes adultos disponibles a nivel mundial de Gato Andino (presentando el primer ejemplar hembra) y 42 cráneos de Gato del Pajonal. En el presente estudio casi duplicamos la cantidad de información disponible acerca de las medidas externas de especímenes frescos para Gato Andino y proveemos medidas y fotos de los 6 cráneos disponibles de adultos de Gato Andino a nivel mundial incluyendo 2 nuevos de sexo conocido. Los datos muestran que el Gato Andino es de mayor tamaño y las diferencias morfométricas podrían estar relacionadas al dimorfismo sexual en ambas especies. El Análisis de Componentes Principales, separa casi por completo al Gato Andino del Gato del Pajonal.

Key words: Argentina, carnivore, *Leopardus colocolo*, *Leopardus jacobita*, morphology, sexual dimorphism, skull

Despite the increasing number of studies on *Leopardus jacobita*, the endangered Andean cat (IUCN—Villalba et al. 2018), basic biological traits are still unknown for this species (AGA 2011). The Andean cat shares all of its distributional range with the Pampas cat (*Leopardus colocolo*), which is more widely distributed and more abundant than *L. jacobita* (AGA 2011;

Reppucci 2012). The study of these congeneric species in sympatry is especially interesting given that they may be competing for the same resources (Johnson et al. 1998; Lucherini and Luengos Vidal 2003; Walker et al. 2007).

The lack of information on the morphometrics of these species is a consequence of: 1) small sample size of currently available specimens; 2) sexes of most of the previously studied specimens were unknown (e.g., Salles 1992; Yensen and Seymour 2000; García-Perea 2002; Sunquist and Sunquist 2002); 3) museum specimens, the basis of most previous research, typically comprise a single part of the body, either the skull or the skin; 4) museum skins often lack field measurements; and 5) the sizes of skins change due to tanning methods (Yensen and Seymour 2000).

Most of the previously published morphometric data for the Andean cat were derived from museum skins and skulls. From 1865 to 2006, external measurements of only 6 fresh specimens of Andean cats were reported in the literature (Salles 1992; Yensen and Seymour 2000; García-Perea 2002; Sunquist and Sunquist 2002; Villalba 2006), and there were only 4 skulls of adult specimens in mammal collections worldwide, only 1 of them of known sex. Furthermore, the Andean cat has been largely excluded from analyses of felid skulls because of scarcity of material (e.g., Werdelin 1983; Christiansen 2008; Sicuro and Oliveira 2011; Tamagnini et al. 2017).

Mammalian carnivore morphology is related to many aspects of their natural history, including physiological and ecological traits. Body size of carnivores in particular (Lindstedt et al. 1986; McNab 1989; Carbone et al. 1999; Bonner 2011) strongly affects predatory behavior and predator–prey interactions as well as intraguild interactions, thus ultimately influencing the composition of vertebrate communities (Rosenzweig 1968; Banse and Mosher 1980; Dayan and Simberloff 1994; Lewis et al. 2008).

In this study, we provide new morphological data derived from the largest sample of live Andean and Pampas cats ever studied in sympatry and from the first known adult female Andean cat skull as well as a second adult male. We assess intraspecific sexual dimorphism for both species and contrast skull morphological variation of Andean cats with Pampas cats.

Materials and Methods

Analyses of live animals.—Animals were trapped in the western part of Jujuy Province, Argentina (22°30′S, 66°30′W). This area forms part of the High Andes ecoregion that encompasses a mosaic of mountain ranges, volcanoes, salt flats, lagoons, and high-elevation plateaus. Elevation of the study area ranged from 3,500 to 6,000 m above sea level with an average of 4,200 m. Topography of the terrain varied markedly, with numerous canyons and large areas with little topographical relief and isolated cliffs. The vegetation was typically comprised of sparse scrubland steppes and grassy steppes, with some wet areas comprised of cushion bogs. The annual rainfall varied from 100 to 200 mm and was concentrated in the summer (January and February).

Andean and Pampas cats were captured between September 2011 and May 2016. We used Victor Soft Catch 1 1/2 (Oneida Victor, Euclid, Ohio) foot hold traps and iron mesh box traps. Cats were immobilized with a combination of Ketamine and Medetodomidine, later reversed using Atipamezole. Capture and handling procedures followed the guidelines of the American Society of Mammalogists (Sikes et al. 2016) and were authorized by the Secretaría de Biodiversidad, Jujuy Province government.

On the basis of tooth wear and external characteristics (i.e., mammary gland condition for females), we assigned the animals to 3 estimated age classes: juveniles, subadults, and adults (Zapata et al. 1997; Gipson et al. 2000; Luengos Vidal et al. 2009). We measured 16 external variables (Fig. 1) and calculated the ratio between tail length and head and body length (TL/HBL) for comparison with previous studies. Cats were weighed to the nearest 0.1 kg with a 10-kg spring balance (Pesola, PESOLA AG, Baar, Switzerland). Tooth, ear, foot, and skull measurements were taken to the nearest 0.1 cm with a vernier caliper. Other external measurements were taken to the nearest 0.1 cm with a measuring tape. For cats captured more than once, only the first measurements were used in the analysis. Because of logistical constraints and safety issues, we could not take all measurements in some cases.

Because sample sizes were small, we used only descriptive statistics to assess possible trends for body measurements. We report the mean, median, interquartile range, and *SD* for each measurement.

Analyses of dry skulls.—We used 18 morphometric variables to describe form and function of skull characters based on Morales and Giannini (2010; but see also García-Perea 2002), and 6 additional measurements (Fig. 1). These measurements were obtained for all 6 skulls of adult Andean and 42 Pampas cats. Pampas cats are recognized as a single species (Kitchener et al. 2017), although some have suggested the existence of 3 species based on skull morphology (García-Perea 1994). We pooled all individuals for the analyses, but retained individual designations for the 3 forms described by García-Perea (1994; *L. braccatus*, *L. colocolo*, and *L. pajeros*) when possible. Specimens used in the analysis are listed in Appendix I.

Although scarce, collection localities for all Andean cat skulls represent almost the entire latitudinal range of the species (Appendix I). We selected 4 measurements: condylobasal length (CBL), zygomatic breadth (ZB), postorbital constriction (PoC), and fossa temporalis length (FTL) to visually assess patterns of size and shape variation along latitudinal gradients. Second, we assessed sexual dimorphism in both species. For the Andean cat, we used descriptive statistics to contrast all 18 measurements between individual *L. jacobita* skulls and skulls of known females and males of *L. colocolo*. Additionally, we assessed sexual dimorphism in *L. colocolo* using a Mann–Whitney *U*-test for all 18 measurements with program InfoStat version 2016 (Di Rienzo et al. 2016). We performed a principal component analysis (PCA) of both felid species using a reduced set of measurements: CBL, load arm of the canine (CG, measured at the upper canine, which reflects the true load

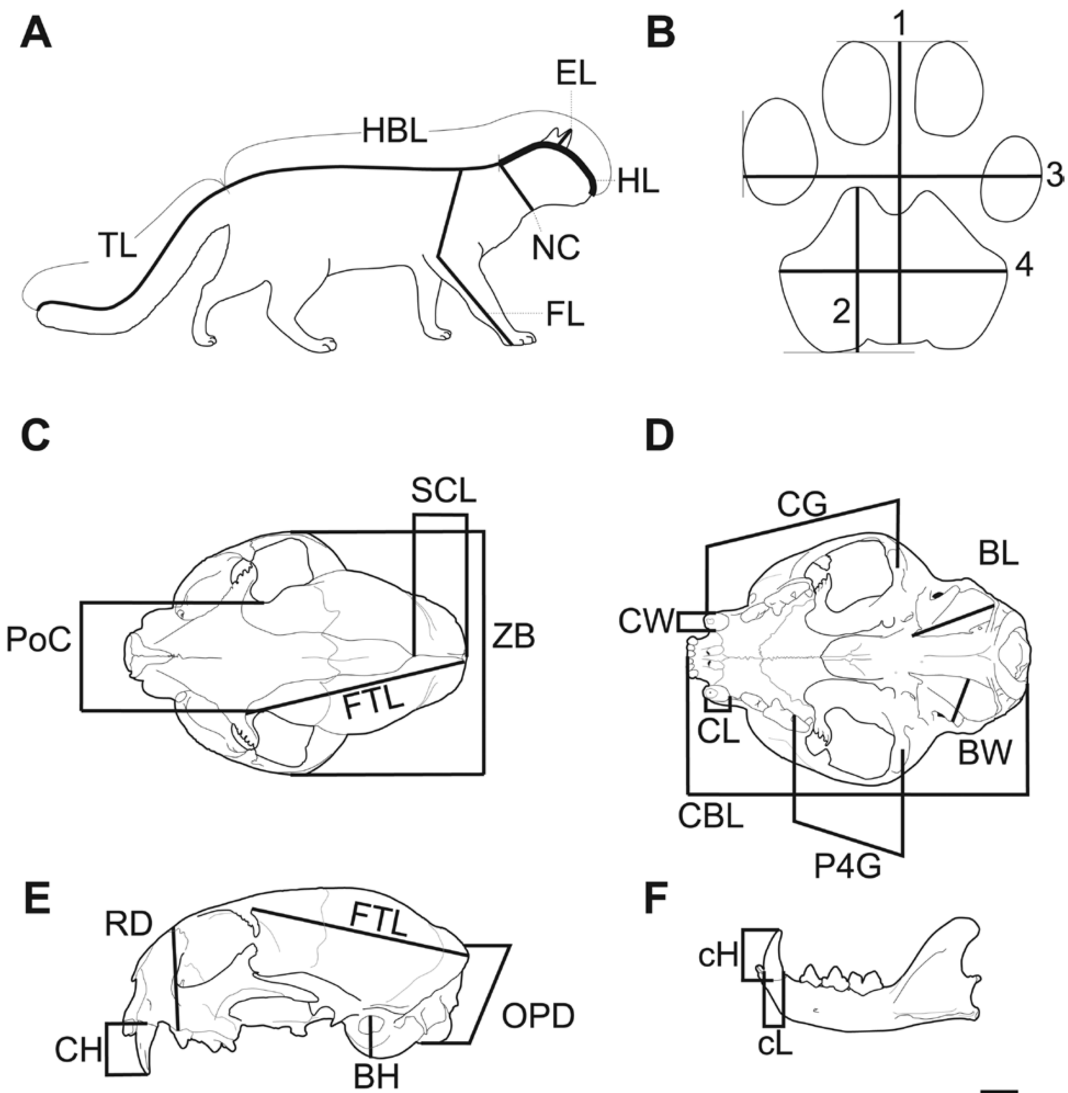

Fig. 1.—External and dry skull measurements used in this study. External measurements: A) HBL, head body length; EL, ear length; HL, head length; NC, neck circumference; FL, fore-leg length; TL, tail length. B) 1, total pad length; 2, metacarpal pad length; 3, total pad width; and 4, metacarpal pad width. Skull: C) PoC, postorbital constriction; ZB, zygomatic breadth; SCL, sagittal crest length; FTL, fossa temporalis length. D) BL, bulla length; BW, bulla width; CBL, condylobasal length; P4G, load arm of the carnassial; CW, upper canine width; CG, load arm of the canine; CL, upper canine length. E) CH, upper canine height; RD, rostral depth; BH, bulla height; FTL, fossa temporalis length; OPD, occipital plate depth. F) cH, lower canine height; cL, lower canine length.

arm at the dentary on the lower canine, as it occludes with the upper canine), upper canine length (CL), upper canine width (CW), FTL, occipital plate length (OPD), load arm of the carnassial (P4G, measured at the upper canine; see CG above), PoC, and ZB. These were selected because they provide the best trade-off between size and shape descriptors of skulls and the number of specimens included in the analysis ($n = 42$). PCA was performed using the variance–covariance matrix in program PAST version 3.12 (Hammer et al. 2001).

Finally, we performed a stepwise discriminant function analysis with forward variable selection using the Wilks' lambda criterion in an effort to identify variables most effective in discriminating between skulls of each species. We then used these variables in a canonical discriminant analysis (CDA—Mardia et al. 1979) to assess the ability of the selected model to correctly identify the species. This analysis included all 6 Andean cat skulls and 42 Pampas cat skulls. We used the MASS, klaR, candisc packages (Venables and Ripley 2002; Weihs et al. 2005; Friendly and Fox 2017) in Program R 3.4.1 (R Development Core Team 2017).

Results

Analyses of live animals.—We livetrapped 5 Andean cats (2 males and 3 females) and 6 Pampas cats (3 males and 3 females). Ten individuals were adults, and 1 was a subadult Pampas cat. External measurements for all captured cats are provided in Supplementary Data SD1. External measurements of male and female Andean cats were larger than those of Pampas cats for body mass, head and body length, tail length, foot size, and external and distal distances between canines (Supplementary Data SD1). Males of both species were larger than the corresponding females for head and body length, tail length, foot size, and external and distal distances between canines (Supplementary Data SD1). The ratio of tail length to head and body length (TL/HBL) differed between species as well as between sexes for Andean cats (mean ± *SD*; Andean cats, females: 70.1 ± 3.45, males: 61.2 ± 0.16; Pampas cats, females: 47.4 ± 2.29, males: 49.5 ± 0.45).

Analyses of dry skulls.—Skull measurements for every specimen of Andean cat and measurement ranges for skulls of female, male, and unknown sex Pampas cats are provided in Supplementary Data SD2 and photos of all 6 available skulls of adult Andean cats are provided in Supplementary Data SD3 and Fig. 2. We report measurements for 1 female Pampas cat that died from natural causes during the sampling period in the study area.

Skull morphology of Andean cats did not show any trend or pattern of variation associated with latitude (Supplementary Data SD2). Skulls of known sex for *L. jacobita* showed a pattern suggesting sexual dimorphism is present in this species (Fig. 2). Skull measurements suggested that males were larger than females in CBL, lower canine height (cH), upper canine height (CH), loading arm of the canine (CG), FTL, P4G, rostral depth (RD), and sagittal crest length (SCL). However, they were similar in bulla length (BL), bulla width (BW), lower canine length (cL), CL, cW, CW, OPD, and ZB, and smaller in bulla height (BH) and PoC (Supplementary Data SD2). For Pampas cats, descriptive statistics showed the same pattern observed in *L. jacobita*. The Mann–Whitney tests revealed

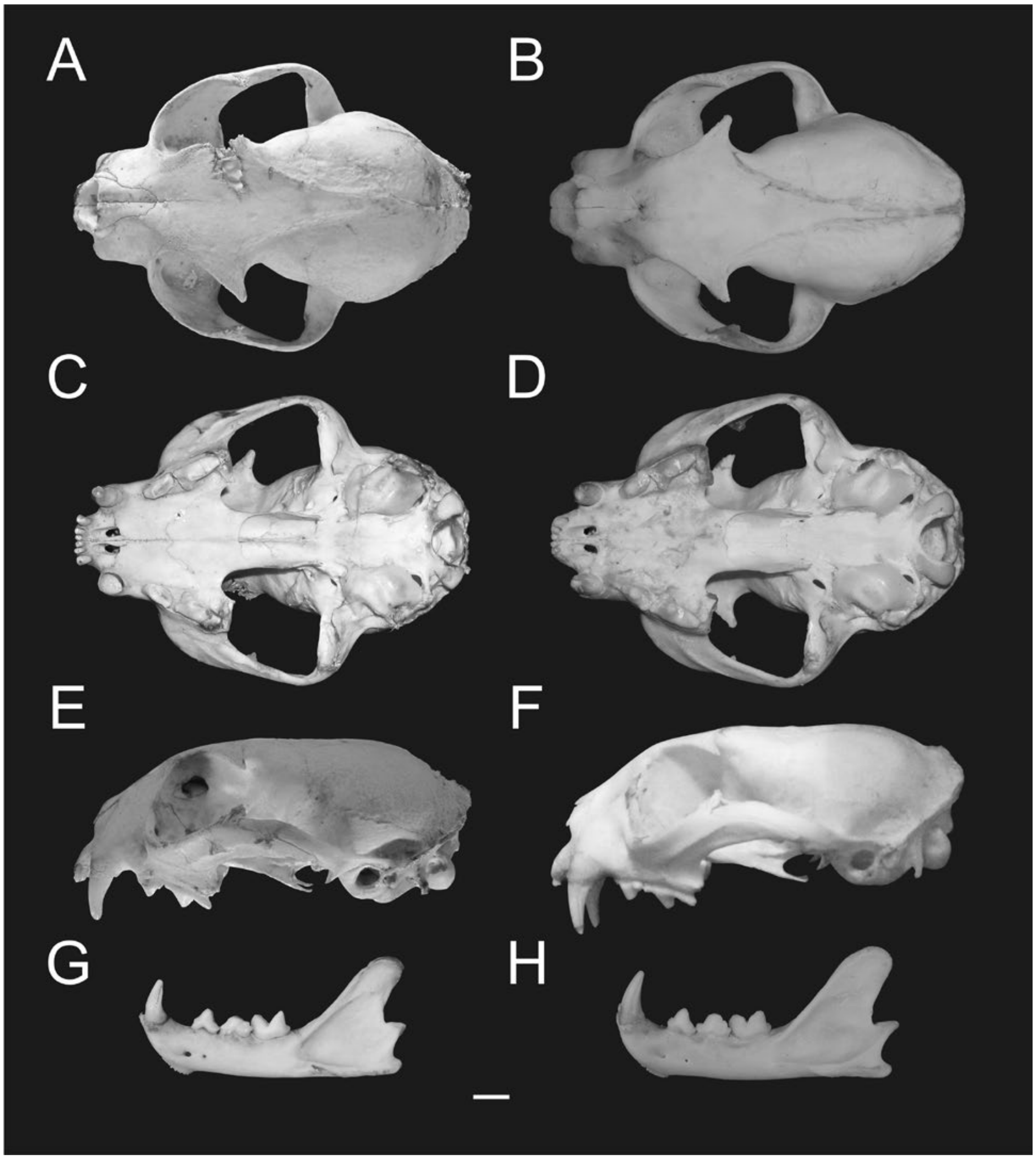

Fig. 2.—Skulls and mandibles of the 2 specimens of adult *Leopardus jacobita* collected from the High Andes, northwest Argentina: CGEM 401, first Andean cat skull known to be a female (A, C, E, G); CGEM 400, male (B, D, F, H). Views: dorsal (A, B); ventral (C, D); lateral (E, F); and lateral of the mandible (G, H). Scale bar = 10 mm.

significant differences for 5 skull metrics: cH, CH, cL, and CL being larger in males and BH being larger in females. Thus, *L. colocolo* females exhibited larger canines (longer craniocaudally) and higher canines than males, while males had higher bullae. When measurements were compared between species (Supplementary Data SD2), skulls tended to be longer in Andean cats than Pampas cats (CBL) although there was some overlap between small Andean cat females (CGECM 401 and MUSM 6015, a suspected female; see García-Perea 2002:115) and large Pampas cat males.

PC1 accounted for 86.1% of the variation in skull measurements, with greatest loadings associated with variables CBL, ZB, and CG. The second principal component accounted for 7.3% of the variation, with the greatest loading associated with FTL (Table 1). For this component, there was some sphericity with respect to CBL and ZB. The scatter diagram for the first 2 principal components (Fig. 3) showed almost complete separation between Andean cats and *L. colocolo*, and within *L. colocolo*, *L. braccatus* was largely separated from *L. colocolo* and *L. pajeros* (sensu García-Perea 1994; Fig. 3).

Finally, stepwise discriminant function analysis with forward selection using Wilks' lambda to assess overall model significance showed P4G, RD, and CG as the most effective variables in predicting species membership of each skull (Table 2). With 3 variables in the analysis, there was significant discrimination between the 2 felid species (Table 2). The squared canonical correlation was 0.81 and had an eigenvalue of 4.33. The canonical correlation was different from zero ($F_{1,38}$ = 54.8, $P < 0.001$). The correlations between the variables and the canonical axis were −0.83, −0.19, and −0.70 for CG, RD, and P4G, respectively.

Discussion

We provide new morphological material and data for 2 rare felids, including the Andean cat. Our external measurements for live Andean cats, measurements and photos for all 6 available skulls of adult Andean cats, and the first known female specimen demonstrate the presence of species-specific characteristics. In particular, we found that external measurements for some adult Andean cats had values for head–body length and tail length that were equivalent to those for the subadult class proposed by García-Perea (2002). Clearly, the age-class criteria based on external measurements should be reevaluated. On the other hand, the ratio of tail length to head and body size was relatively constant for both species regardless of age class. Tail length was about 66–75% of the head and body length for the Andean cat and less than 50% for the Pampas cat, and thus provides a reliable metric with which to discriminate between the 2 species.

Among the skull characters proposed by García-Perea (2002) to distinguish between Andean and Pampas cats, sagittal crest length does not appear to be a reliable character. We recorded sagittal crest lengths in several Pampas cats that were similar to or even longer than the longest crests found among Andean cat skulls (e.g., FMNH 24370; CGECM 402). Because this is an age-dependent character, we suggest that caution must be used when species identification is based on this character.

Both species exhibited sexual size dimorphism based on external and skull measurements, with males being generally larger than females (e.g., weight, head and body length, and CBL). Surprisingly, within Pampas cats, female skulls tended to have higher canines (cH, CH), while males tended to have higher tympanic bullae (BH). In Andean cats, skulls were larger in males than females with respect to CBL and FTL (among others, see Supplementary Data SD2), but had similar ZB and smaller PC measurements, making male skulls narrower, but with a greater surface area available for origin of the temporal muscle, which adducts the mandible (see, e.g., Christiansen and Adolffsen 2005; Morales and Giannini 2010). Among Andean cats, with the exception of the thinner skulls in males, the observed differences are typical for dimorphic felid skulls (see, e.g., Sicuro and Oliveira 2011). Additional specimens would be useful in corroborating this assertion. Furthermore, our data indicate that Andean cats are larger and heavier than Pampas cats, and that they differ craniometrically. Within the skull morphospace (Fig. 3), Andean cats were more similar to allopatric *L. braccatus* than to more sympatric *L. colocolo* and *L. pajeros* (sensu García-Perea 1994). The latter forms had more rounded skulls (based on PC2) than *L. jacobita* and *L. braccatus*. Stepwise discriminant functions and CDA identified CG, P4G, and RD as useful variables in the discrimination of *L. colocolo* and *L. jacobita*: the first 2 of these measurements represent the load arms of the carnassials and the canines (as they are almost identical to their respective lower teeth; see "Materials and Methods"); being shorter, they provide some mechanical advantage in *L. colocolo*.

Although the Andean cat is a specialist (restricted food and spatiotemporal niches) and occurs at lower population densities than the Pampas cat, there is wide trophic and spatiotemporal niche overlap between these species (Walker et al. 2007; Napolitano et al. 2008; Tellaeche 2010; Reppucci et al. 2011; Reppucci 2012). Long tails in felids and other mammals have been associated with arboreality and sprinting (e.g.,

Table 1.—Results of the principal component analysis ($n = 42$) of skull measurements of Andean cats (*Leopardus jacobita*) and Pampas cats (*L. colocolo*): eigenvectors, eigenvalues, and percentage of variation explained by the each of the first 3 axes. See text for acronyms of variables.

Eigenvectors	PC1	PC2	PC3
PoC	−0.007	−0.123	−0.148
CBL	0.608	−0.526	0.095
ZB	0.487	0.432	−0.738
CG	0.424	−0.288	0.097
P4G	0.265	−0.043	0.199
CW	0.044	−0.019	−0.034
CL	0.051	−0.041	−0.061
FTL	0.357	0.62	0.485
OPD	0.105	0.224	0.369
Eigenvalue	96.483	7.273	3.76
Variance	86.096	6.49	3.355

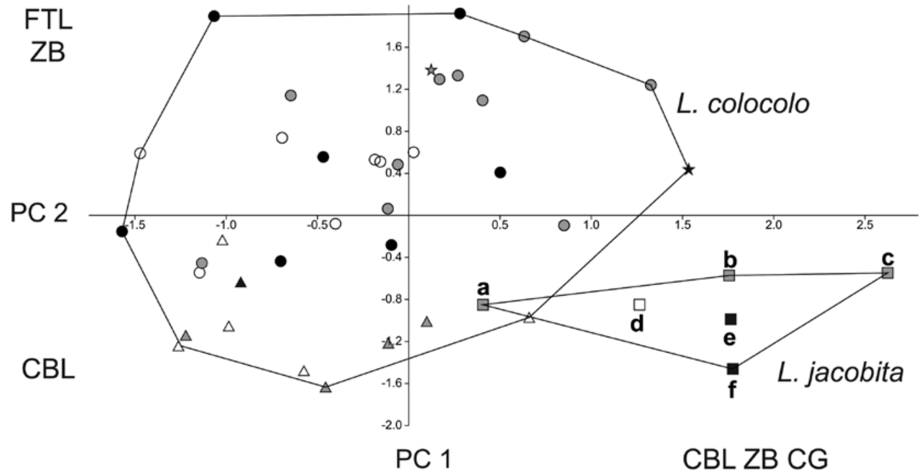

Fig. 3.—Scatter diagram for the first 2 principal components (PCs; specimen scores scaled to unit eigenvector). Circles: *Leopardus pajeros*; stars: *L. colocolo*; triangles: *L. braccatus* (all 3 sensu García-Perea 1994); squares: *L. jacobita*. Open symbols: females; black solid figures: males; gray solid figures: specimens of unknown sex. Species are delineated with convex polygons. Letters indicate different Andean cat individuals (a: MUSM 6015, b: GECM 27, c: CBF 445, d: GECM 401, e: GECM 400, f: APN). Variables mentioned are those with larger values in the respective PC. For acronyms of variables, see Fig. 1.

Table 2.—Results of the stepwise forward variable selection discriminant function analysis to distinguish between skulls of Andean cats (*Leopardus jacobita*) and Pampas cats (*L. colocolo*). Variables selected and corresponding Wilks' lambda, *F*.statistic, and *P*-value for each variable (*F*.statistics.overall: approximated *F*-statistic for the model to this point and its significance [*P*-value.overall]) and for each added variable in the model (*F*.statistics.diff: approximated *F*-statistic for comparing the model including the new variable with the model not including it and its significance test [*P*-value.diff]).

Variables	Wilks' lambda	*F* statistics overall	*P*-value overall	*F* statistics diff	*P*-value diff
CG	0.26	43.69	< 0.01	43.69	< 0.01
RD	0.10	62.43	< 0.01	21.49	< 0.01
P4G	0.07	56.68	< 0.01	5.45	< 0.01

margay, *Leopardus wiedii* and cheetah, *Acinonyx jubatus*, respectively—Thompson 1945; Sunquist and Sunquist 2002; Kitchener et al. 2010), but are also a typical trait for the snow leopard (*Panthera uncia*), a larger felid that occurs in rocky habitats similar to those of the Andean cat. In snow leopards, the long tail appears to assist balance while moving along steep slopes and may provide insulation from cold for the face and paws at high altitudes when resting (Kitchener et al. 2010). The Andean cat is restricted to areas with cold nights, whereas Pampas cats occur in more varied climates (e.g., Sunquist and Sunquist 2002, 2009). When sympatric, Andean cats appear to be more strictly associated with rocky areas than Pampas cats (Tellaeche 2015). Thus, it is reasonable to infer that differences in body size and shape, particularly the longer tail of Andean cats, could be advantageous while hunting and moving in steep rocky habitats and for thermoregulation as well.

Acknowledgments

We are grateful to the veterinarians who helped with the animal captures: P. Cuervo, A. Mutlow, H. Mutlow, D. Kenny, N. Boedeker, A. Atkins, S. J. Hwang, P. Alcazar, D. Clifford, A. Alexander, and S. Zavala. We thank M. Monteverde (CEAN) for the measurements of the skull from Chihuidos, and A. Novaro (CONICET) and S. Walker (WCS) who collected this skull. We thank P. Perovic and all the volunteers and villagers who contributed to data collection and S. Kennerknecht for his help with the English review of the manuscript. We acknowledge all curators and personnel involved in all collections visited (institutions in alphabetical order): U. Pardiñas (CNP); J. Aparicio, J. Tordoya (CBF); R. Ojeda (CMI); R. Barquez, M. Díaz (CML); M. Carrera (MC); D. Hernández (ZVC-M); L. Heaney, W. Stanley (FMNH); D. Flores, V. Segura, P. Teta, S. Lucero (MACN); V. Pacheco, C. Tello (MUSM); D. Verzi, I. Olivares, C. Morgan (MLP); E. González, Y. Hernández, J. González (MNHN); D. Wilson, D. Lunde, K. M. Helgen, J. Ososky; A. L. Gardner, L. Gordon, J. Jacobs (USNM). Thanks to J. Scheibe for greatly improving this manuscript with his comments and to R. Moyano for her help. MMM thanks a Short Term Visitor Fellowship from the Smithsonian Institution, PICT 0708-2015, and PICT 2389-2015. We acknowledge governmental institutions, CONICET, and DBByF of Universidad Nacional del Sur (especially E. Casanave).

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Morphometric measurements of individual Andean (*Leopardus jacobita*) and Pampas cats (*L. colocolo*). For each sex and species, the mean, median, interquartile range (IQR), and *SD* are reported. Abbreviations and symbols: AC = Andean cat; PC = Pampas cat; F = female;

M = male; BM = body mass (kg); DBC = external and distal distance between canines (mm): from the gum line of C1 left to the gum line of C1 right; HBL = head–body length (cm): from the tip of the nose to the base of the tail at the notch of the sacrum; TL = tail length (cm): from the base of the tail at the rump to the tip of the last caudal vertebra; HL = head length (cm), from the top of the occipital bone (notch in back of skull) to nose tip; FL = fore-leg length (cm): from the most dorsal point of scapula to the base of the foot; EL = ear length (cm): from base to tip, fur excluded; NC = neck maximum circumference (cm); FPL = front right pad length (mm, 4 measurements: 1 = total pad length, 2 = metacarpal pad length, 3 = total pad width, and 4 = metacarpal pad width); BLP = back left pad length (mm, 4 measurements: 1 = total pad length, 2 = metatarsal pad length, 3 = total pad width, and 4 = metatarsal pad width).

Supplementary Data SD2.—Values (mm) of skull and teeth variables measured on all the specimens of Andean cat (*Leopardus jacobita*) and range of measurements for all the specimens of Pampas cat (*L. colocolo*). For males, females, and unknown sex Pampas cat, the mean, median, interquartile range (IQR), and *SD* are reported.

Supplementary Data SD3.—Skulls and mandibles of adult specimens of Andean cat (*Leopardus jacobita*) from the following collections: APN (A, E, I, M); CBF 445 (B, F, J, N); CGEM 27 (C, G, K, O); MUSM 6015 (D, H, L, P). Views: dorsal (A–D), ventral (E–H), lateral (I–L), and lateral of the mandible (M–P). Scale bar = 10 mm

Literature Cited

AGA. 2011. Plan Estratégico para la Conservación del Gato Andino. 2011–2016. Andean Cat Alliance, La Paz, Bolivia.

Banse, K., and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecological Monographs 50:355–379.

Bonner, J. T. 2011. Why size matters: from bacteria to blue whales. Princeton University Press, Princeton, New Jersey.

Carbone, C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.

Christiansen, P. 2008. Evolution of skull and mandible shape in cats (Carnivora: Felidae). PLoS One 3:e2807.

Christiansen, P., and J. S. Adolfssen. 2005. Bite forces, canine strength and skull allometry in carnivores (Mammalia, Carnivora). Journal of Zoology 266:133–151.

Dayan, T., and D. Simberloff. 1994. Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. Ecology 75:1063–1073.

Di Rienzo, J. A., F. Casanoves, M. G. Balzarini, L. Gonzalez, M. Tablada, and C. W. Robledo. 2016. InfoStat versión 2016. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Córdoba, Argentina. http://www.infostat.com.ar.

Friendly, M., and J. Fox. 2017. Candisc: visualizing generalized canonical discriminant and canonical correlation analysis. R package version 0.8-0.

García-Perea, R. 1994. The Pampas cat group (genus *Lynchailurus* Severtzov, 1858) (Carnivora, Felidae): a systematic and biogeographic review. American Museum Novitates 3096:1–35.

García-Perea, R. 2002. Andean mountain cat, *Orealurus jacobita*: morphological description and comparison with other felines from the altiplano. Journal of Mammalogy 83:110–124.

Gipson, P. S., W. B. Ballard, R. M. Nowak, and L. D. Mech. 2000. Accuracy and precision of estimating age of gray wolves by tooth wear. The Journal of Wildlife Management 64:752–758.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Paleontologia Electronica 4:1–9.

Johnson, W. E., M. Culver, J. A. Iriarte, E. Eizirik, K. L. Seymour, and S. J. O'Brien. 1998. Tracking the evolution of the elusive Andean mountain cat (*Oreailurus jacobita*) from mitochondrial DNA. The Journal of Heredity 89:227–232.

Kitchener, A. C., B. Van Valkenburgh, and N. Yamaguchi. 2010. Felid form and function. Pp. 83–106 in Biology and conservation of wild felids (D. W. Macdonald and A. J. Loveridge, eds.). Oxford University Press, New York.

Kitchener, A. C., et al. 2017. A revised taxonomy of the Felidae: the final report of the Cat Classification Task Force of the IUCN Cat Specialist Group. Cat News.

Lewis, H. M., R. Law, and A. J. McKane. 2008. Abundance-body size relationships: the roles of metabolism and population dynamics. The Journal of Animal Ecology 77:1056–1062.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology 67:413–418.

Lucherini, M., and E. Luengos Vidal. 2003. Intraguild competition as a potential factor affecting the conservation of two endangered cats in Argentina. Endangered Species Update 20:211–220.

Luengos Vidal, E. M., M. Lucherini, E. B. Casanave, and C. Sillero Zubiri. 2009. Morphometrics of Pampas foxes (*Pseudalopex gymnocercus*) in the Argentine Pampas. Mammalia 73:63–67.

Mardia, K. V., J. T. Kent, and J. M. Bibby. 1979. Multivariate analysis. Academic Press, New York.

McNab, B. K. 1989. Basal rate of metabolism, body size, and food habits in the order Carnivora. Pp. 335–354 in Carnivore behavior, ecology, and evolution (J. L. Gittleman, ed.). University of Tennessee, Springer Science & Business Media, Knoxville.

Morales, M. M., and N. P. Giannini. 2010. Morphofunctional patterns in Neotropical felids: species co-existence and historical assembly. Biological Journal of the Linnean Society 100:711–724.

Napolitano, C., et al. 2008. Ecological and biogeographical inferences on two sympatric and enigmatic Andean cat species using genetic identification of faecal samples. Molecular Ecology 17:678–690.

R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reppucci, J. I. 2012. Ecología y abundancia poblacional del gato andino (*Leopardus jacobita*) y gato del pajonal (*L. colocolo*) en los altos Andes Argentinos. Ph.D. dissertation, Universidad Nacional del Sur, Bahía Blanca, Argentina.

Reppucci, J., B. Gardner, and M. Lucherini. 2011. Estimating detection and density of the Andean cat in the high Andes. Journal of Mammalogy 92:140–147.

Rosenzweig, M. L. 1968. The strategy of body size in mammalian carnivores. American Midland Naturalist 80:299–315.

Salles, L. O. 1992. Felid phylogenetics: extant taxa and skull morphology (Felidae, Aeluroidea). American Museum Novitates 3047:1–67.

Sicuro, F. L., and L. F. B. Oliveira. 2011. Skull morphology and functionality of extant Felidae (Mammalia: Carnivora): a phylogenetic and evolutionary perspective. Zoological Journal of the Linnean Society 161:414–462.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Sunquist, M., and F. C. Sunquist. 2002. Wild cats of the world. University of Chicago Press, London, United Kingdom.

Sunquist, M. E., and F. C. Sunquist. 2009. Family Felidae. Pp. 54–168 in Handbook of mammals of the world, vol. 1. Carnivores. Lynx Editions, Barcelona, Spain.

Tamagnini, D., C. Meloro, and A. Cardini. 2017. Anyone with a long-face? Craniofacial Evolutionary Allometry (CREA) in a family of short-faced mammals, the Felidae. Evolutionary Biology 44:476–495.

Tellaeche, C. G. 2010. Análisis de hábitos alimenticios de dos especies de felinos simpátricos (*Leopardus jacobita* y *Leopardus colocolo*). Graduate thesis, Universidad Nacional del Sur, Bahía Blanca, Argentina.

Tellaeche, C. G. 2015. Ecología y uso del espacio de dos especies de félidos, Gato Andino (*Leopardus jacobita*) y Gato del Pajonal (*L. colocolo*) en la región Altoandina, Prov. de Jujuy. Ph.D. dissertation, Universidad Nacional del Sur, Bahía Blanca, Argentina.

Thompson, D. W. 1945. On growth and form. Cambridge University Press, Cambridge, United Kingdom.

Venables, W. N., and Ripley, B. D. 2002. Modern applied statistics with S. 4th ed. Springer, New York.

Villalba, M. L. 2006. Ecology and behaviour of two sympatric felids, the Andean cat (*Oreailurus jacobita*) and Pampas cat (*Oncifelis colocolo*) in Khastor (Southern Bolivia). Pp. 1–5 in Cat project of the month. UICN, SSC, Cat Specialist Group, General Technical Report.

Villalba, L., et al. 2018. *Leopardus jacobita*. In: IUCN 2015. The IUCN Red List of Threatened Species 2018: e.T15452A50657407. http://dx.doi.org/10.2305/IUCN.UK.20161.RLTS.T15452A50657407.en. Accessed 15 January 2018.

Walker, S. R., et al. 2007. Diets of three species of Andean carnivores in high-altitude deserts of Argentina. Journal of Mammalogy 88:519–525.

Weihs, C., U. Ligges, K. Luebke, and N. Raabe. 2005. klaR analyzing German business cycles. Pp. 335–343 in Data analysis and decision support (D. Baier, R. Decker, and L. Schmidt-Thieme, eds.). Springer-Verlag, Berlin, Germany.

Werdelin, L. 1983. Morphological patterns in the skulls of cats. Biological Journal of the Linnean Society 19:375–391.

Yensen, E., and K. L. Seymour. 2000. *Oreailurus jacobita*. Mammalian Species 664:1–6.

Zapata, S. C., M. C. Funes, and A. J. Novaro. 1997. Estimación de la edad en el zorro colorado patagónico (*Pseudalopex culpaeus*). Mastozoología Neotropical 4:145–150.

Submitted 5 November 2017. Accepted 7 June 2018.

Associate Editor was John Scheibe.

Appendix I

Taxa are organized in alphabetical order by genus and species. The number of specimens examined follows the species name. Specimens are classified according to sex (female, male, unknown); the number of specimens for each sex category is reported in parentheses. For each specimen we detail the collection and catalog number. An asterisk (*) indicates the specimen was not included in the PCA analysis. Collection localities are given only for *Leopardus jacobita*.

The following mammal collections were visited for this work: **Argentina**: APN, Centro de Ecología Aplicada-Dirección de Parques Nacionales, Junín de los Andes; CGECM, Colección del Grupo de Ecología Comportamental de Mamíferos, Bahía Blanca; CMI, Colección de Mamíferos del Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza; CML, Colección Mamíferos Lillo, Tucumán; CNP, Centro Nacional Patagónico, Puerto Madryn; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”; MC, Private Collection Marcelo Carrera, Puerto Madryn; MLP, Museo de La Plata, La Plata; **Bolivia**: CBF, Colección Boliviana de Fauna, La Paz; **Perú**: MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima; **United States**: FMNH, Field Museum of Natural History, Chicago; USNM, National Museum of Natural History, Washington, DC; **Uruguay**: MNHN, Museo Nacional de Historia Natural, Montevideo; ZVC-M, Colección Zoología de Vertebrados, Facultad de Ciencias, Universidad de la República, Montevideo.

(in alphabetical order): Centro Nacional Patagónico, Puerto Madryn, Argentina (CNP); Colección Boliviana de Fauna, La Paz, Bolivia (CBF); Colección de mamíferos of the Centro de Ecología Aplicada, Junín de los Andes, Argentina (Dirección de Parques Nacionales; APN- provisional acronym); Colección de Mamíferos of the Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina (CMI); Colección del Grupo de Ecología Comportamental de Mamíferos, Bahía Blanca, Argentina, Universidad Nacional del Sur (CGECM); Colección Mamíferos Lillo, Tucumán, Argentina (CML); Private Collection Marcelo Carrera, Puerto Madryn, Argentina (MC); Colección Zoología de Vertebrados, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (ZVC-M); Field Museum of Natural History, Chicago, United States (FMNH); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina (MACN); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); Museo de La Plata, La Plata, Argentina (MLP); Museo Nacional de Historia Natural, Montevideo, Uruguay (MNHN); and National Museum of Natural History, Smithsonian Institution, Washington, DC, United States (USNM).

Leopardus braccatus (10)

Female (5): MNHN 1315; MNHN 1375; MNHN 2432; MNHN 2780; MNHN 4705.

Male (1): MNHN 4706.

Unknown sex (4): MNHN 971; MNHN 3224; MNHN 3413; ZVC-M 1492.

Leopardus colocolo (2)

Male (1): FMNH 24370.

Unknown sex (1): USNM 391853.

Leopardus jacobita (6)

Female (1): CGECM 401 (Argentina, Jujuy, Loma Blanca [22°30′S and 66°29′W]; elevation between 4,000 and 4,200 m a.s.l.).

Male (2): APN without number (Argentina, Neuquén, Los Chihuidos [38°14′S and 69°28′W]; killed along the riverside, at an elevation between 600 and 700 m a.s.l.); CGECM 400 (Argentina, Jujuy, Loma Blanca [22°30′S and 66°29′W]; elevation between 4,000 and 4,200 m a.s.l.).

Unknown sex (3): CBF 445 (Bolivia, Sud Lipez, Potosí, Camp. Kastor); CGECM 27 (Argentina, Tucumán, Los Alisos); MUSM 6015 (Perú, Sierra).

Leopardus pajeros (30)

Female (7): CGECM 402; CML 6226; FMNH 68318; MACN 30.103; MC 774; MC 1728; MLP 1913.

Male (8): FMNH 52488; MACN 15582; MACN 16489*; MC 280; MUSM 415; MUSM 417; MUSM 420; MUSM 421.

Unknown sex (15): CBF 6144; CGECM 1; CGECM 22; CMI 6271; CML 3729; CML 6200*; CML 6229; CML 6238*; CNP 574; MACN 17816; MACN 23176*; MUSM 23107; MUSM 23183; MUSM JO 01; MUSM 418.