

Trophic Segregation of Small Carnivorans (Carnivora: Mustelidae and Mephitidae) from the Southern Cone of South America

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Abstract Remarkable adaptations in the Carnivora have evolved as a way of dealing with feeding competition, accentuating hypocarnivorous or hypercarnivorous morphotypes. The Carnivora is a highly successful order with 47 living species in South America. Their history in South America is recent, and includes few lineages that arrived before the Panamanian bridge was completed (procyonids), and others that arrived later (felids, mephitids). Here, we evaluated the trophic segregation of small carnivorans (*Conepatus chinga*, *Galictis cuja*, *Lontra provocax*, *Lyncodon patagonicus*, and the introduced *Neovison vison*) from southern South America, using a geometric morphometric approach, i.e., Principal Component and Canonical Variate Analysis, to study shape variations and *t*-tests to study size variation. We also performed Canonical

Phylogenetic Ordination to study the association between shape, size, diet, and phylogeny. We identified *C. chinga* as the most hypocarnivorous member of the guild, *G. cuja*, *L. patagonicus*, and *N. vison* as hypercarnivores, with *L. provocax* in an intermediate position. Semiaquatic habits segregate *Lontra provocax*, and partially *N. vison*, from other species. Significant differences in size were observed between all species pairs, except *C. chinga* and *N. vison*. Phylogeny accounts for a very important part of morphological variance, with cladogenetic events between mustelids and mephitids responsible for almost 55 % of it. The small carnivoran guild of southern South America is represented by species adapted to different feeding strategies, with *C. chinga* and *L. provocax* preying mainly on invertebrates, *G. cuja* and *L. patagonicus* specifically on small vertebrates, and the non-native *N. vison* with a highly diverse diet.

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Introduction

One of the most remarkable features of the Carnivora is the presence of carnassial teeth, formed by the upper fourth premolar and the first lower molar, in which large crushing surfaces or cutting edges may be accentuated depending on species adaptations (Popowics 2003). In this context, tooth morphology and size are extremely informative about dietary preferences (Dayan et al. 1989a; Van Valkenburgh 2007), including morphotypes that can be described as “hypercarnivorous” to “hypocarnivorous” (Ewer 1973; Van Valkenburgh 2007). It is possible that these adaptations evolved as a response to feeding competition (Van Valkenburgh 1995), which is in turn a strong force shaping ecosystems (Dayan and Simberloff 1998). In this sense, members of a guild (sensu Root 1967) are expected to be

potential competitors (Dayan and Simberloff 1998), or at least, have evolved in such a way that competition would be avoided where sympatric. In this regard, resource partitioning according to prey size had been detected by Dayan and Simberloff (1994) for British and Irish mustelids, but in contrast McDonald (2002) found that prey size did not increase with predator size. According to Davies et al. (2007), co-occurrence of species might be explained by three alternatives: 1) as co-occurring species are adapted to the same environment, they have similar ecomorphology; 2) co-occurring species have different ecomorphology, to avoid competitive interactions; and 3) ecomorphology of co-occurring species is unrelated one to the other.

The history of the Carnivora in South America is quite recent, and started with the arrival of procyonids in the late Miocene (≈ 8 Ma), followed by canids and some mustelids in the late Pliocene (≈ 3 Ma), and was completed with the arrival of felids, ursids, mephitids, and some mustelids in the early Pleistocene, after the Panamanian bridge was completed allowing the Great American Biotic Interchange (Prevosti and Soibelzon 2012). There are around 47 living species of Carnivora in South America, included within the Canidae, Felidae, Procyonidae, Mustelidae, Mephitidae, Ursidae, Otariidae, and Phocidae (Wozencraft 2005; Prevosti and Soibelzon 2012). Small carnivorans (i.e., less than 7 kg) in the southern cone of South America are represented by one species of Mephitidae, Molina's hog-nosed skunk *Conepatus chinga* (Molina, 1782), and five species of Mustelidae, the lesser grison *Galictis cuja* (Molina, 1782), the Patagonian weasel *Lyncodon patagonicus* (Blainville, 1842), the southern river otter *Lontra provocax* (Thomas, 1908), the marine otter *Lontra felina* (Molina, 1782), and one introduced species, the American mink *Neovison vison* (Schreber, 1777) (Wozencraft 2005; Díaz and Lucherini 2006). Several studies have been carried out on the trophic preferences or other ecological aspects of *C. chinga* (Fuller et al. 1987; Travaini et al. 1998; Donadio et al. 2001, 2004; Castillo et al. 2011) and some on morphological or systematic aspects (Van Gelder 1968; Schiaffini et al. 2013a). Literature about the other species is scarcer and includes phylogeographical studies of *L. felina* (Vianna et al. 2010a) and *L. provocax* (Vianna et al. 2010b), distributional studies on *L. patagonicus* (Prevosti and Pardiñas 2001; Schiaffini et al. 2013b), ecological and morphological studies on *G. cuja* (Delibes et al. 2003; Kraus and Rödel 2004; Ercoli et al. 2012), and some studies on trophic preferences of *N. vison* (Valenzuela et al. 2013) and its interactions with native species (Fasola et al. 2009; Valenzuela et al. 2012). Zapata et al. (2008) studied the relative trophic position of each species in a guild that includes (among several others) *C. chinga* and *G. cuja*, identifying the adaptations that best characterize each type of feeder.

Anatomical and/or morphometric studies might help identify trophic segregation patterns among sympatric species, and

could identify the possibility of competitive processes between species, contributing to a better understanding of guild structures and how phylogeny, diet, and habitat are related to mandible and skull shape in these carnivorans. Our objective was to analyze the trophic segregation among small carnivorans from southern South America, derived from geometric morphometric data from skulls and mandibles. We were particularly interested in identifying morphological features that allow segregation or overlap in morphospace, which reflect ecological adaptations (perhaps exaptations sensu Gould and Vrba 1982), and in consequence will strengthen or weaken competition processes.

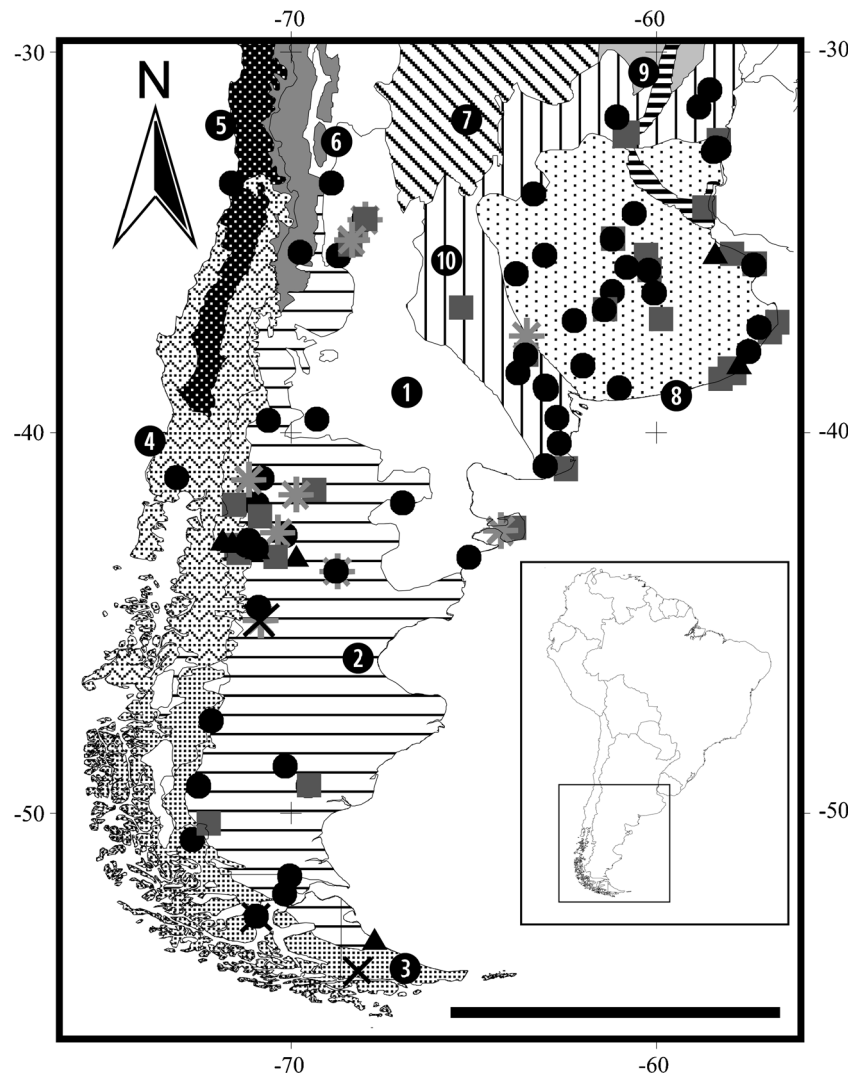
Materials and Methods

Our study area comprised the southern cone of South America, mainly south-central Argentina. According to the biogeographical scheme of Olson et al. (2001), central and southern Argentina includes mainly a large productive temperate grassland (Humid Pampas), temperate-cold rainforests (Valdivian Temperate Forest), and cold, dry areas (Patagonian Steppe and Low Monte, but see also Morello 1985). We selected this area to study guild structure of the species mentioned below, avoiding conflicting areas (e.g., Uruguay and northern Argentina) where other species not included might be present (e.g., *Peronura brasiliensis* (Gmelin, 1788), *Eira barbara* (Linnaeus, 1758), or *Galictis vittata* (Schreber, 1776), see Díaz and Lucherini 2006; Canevari and Vaccaro 2007).

Specimens assigned to *C. chinga*, *G. cuja*, *L. patagonicus*, *L. provocax*, and *N. vison* from the following collections were studied: Colección Mastozoológica del IADIZA (CMI), Mendoza; Fundación Félix de Azara (FFA), Ciudad Autónoma de Buenos Aires; Instituto Miguel Lillo (IML), San Miguel de Tucumán; Instituto Zoológico de la Patagonia (IP), Punta Arenas; Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), Esquel; Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Ciudad Autónoma de Buenos Aires; Museo de Historia Natural de San Rafael (MHNSR), San Rafael; Museo de La Plata (MLP), La Plata; Museo Municipal de Ciencias Naturales “Lorenzo Scaglia” (MMP), Mar del Plata; Naturhistorischen Museum Wien (NMW), Wien; Staatliches Museum für Naturkunde Stuttgart (SMNT), Stuttgart; Universidad Nacional del Sur (UNS), Bahía Blanca. *Lontra felina* was not included in the analyses, owing to its highly different habitat type (mainly the south Pacific coast, Vianna et al. 2010a).

We only analyzed adult specimens, i.e., those with fully erupted dentition and where the basisphenoid-basioccipital suture is not visible (see Van Gelder 1968). We analyzed 133 skulls with known geographical localities of which 84 were *C. chinga*, 27 *G. cuja*, eight *L. patagonicus*, three *L. provocax*, and 11 *N. vison*. We also analyzed 114 mandibles

Fig. 1 Recorded localities for analyzed species: *C. chinga* (black circles), *G. cuja* (grey squares), *L. provocax* (black crosses), *L. patagonicus* (light grey asterisks), and *N. vison* (black triangles). Scale (black bar) represents 1000 km. Numbers represent ecoregions following Olson et al. (2001): 1=Low Monte, 2=Patagonian Steppe, 3=Magellanic Subpolar Forest, 4=Valdivian Temperate Forest, 5=Chilean Matorral, 6=Southern Andean Steppe, 7=Dry Chaco, 8=Humid Pampas, 9=Paraná Flooded Savanna, 10=Espinal



of which 68 were *C. chinga*, 25 *G. cuja*, three *L. provocax*, six *L. patagonicus*, and 12 *N. vison* (Fig. 1, Online Resource 1). The limited number of museum specimens did not allow us to analyze males and females separately. In addition, individuals of *C. chinga* were analyzed together due to a lack of sexual dimorphism (Schiaffini et al. 2013a)

We took digital photographs of skulls in ventral view and right mandibles in lateral view, orienting specimens with the palatal plate and the horizontal ramus parallel to the photographic plane, respectively. We used MakeFan 6 (Sheets 2002) software to position semi-landmarks (Fig. 2), tpsUtil 1.40 (Rohlf 2008a) to compile image files, and tpsDig 2.12 (Rohlf 2008b) to digitalize landmarks and semilandmarks. Landmark configurations were superimposed through Generalized Procrustes Analysis (GPA Goodall 1991; Rohlf 1999). Centroid size was used as size estimator, which is the square root of the summed squared distances of each landmark to the centroid of the form (Zelditch et al. 2004).

Principal Component Analyses (PCA) were performed with MorphoJ v. 1.03b (Klingenberg 2011) and tpsRelw v. 1.35 (Rohlf 2003) software. We also used Canonical Variate Analysis (CVA) to find the differences that best distinguished among the studied species, and its statistical significance was evaluated with Permutation tests and 10000 resamples in MorphoJ v. 1.03b (Klingenberg 2011). Size differences were tested with *t*-tests and Bonferroni correction for independent samples with software R 2.15.3 (R Development Core Team 2013). These analyses were made for both skulls and mandibles.

We used Canonical Phylogenetic Ordination (CPO, Giannini 2003) to test the importance of phylogeny in explaining morphofunctional patterns seen in PCA and CVA, using CANOCO 4.5 (ter Braak and Šmilauer 2002). For shape, we used Procrustes coordinates derived from geometric morphometric analysis (see above), and for phylogeny, an external matrix containing binary variable codes (1 for taxa included in a node, and 0 otherwise) for each node (see Giannini 2003) from

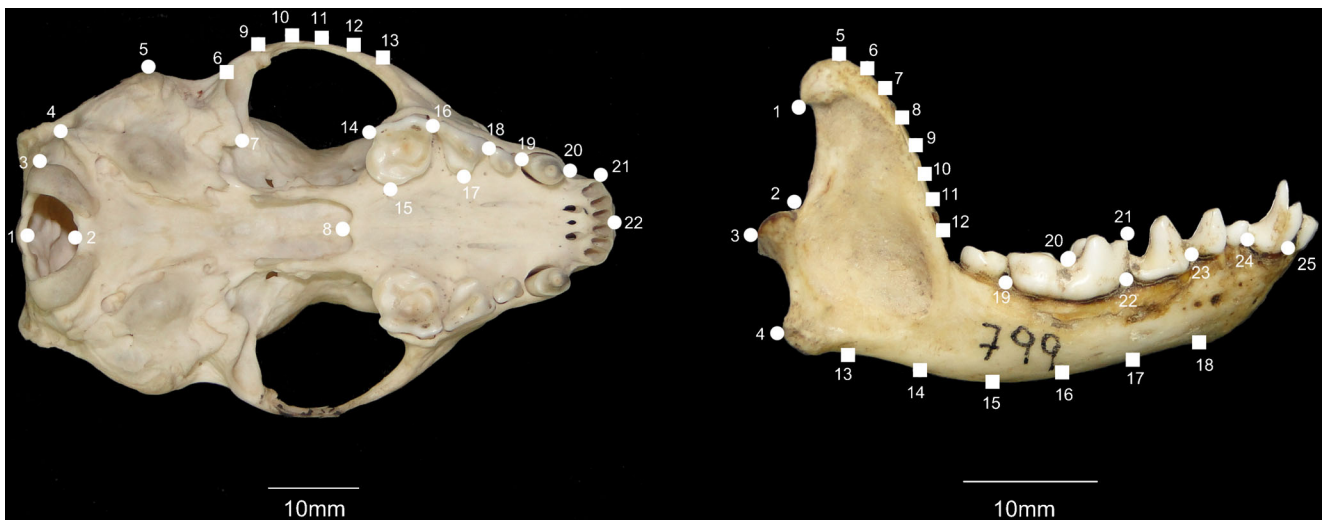


Fig. 2 Landmarks (white circles) and semilandmarks (white squares) on a ventral view of a skull and a lateral view of right mandible (*Conepatus chinga*, LIEB-M-799)

a pruned phylogenetic tree of the group. This tree was derived from Sato et al. (2012) and can be seen in Online Resource 2. We also analyzed the importance of morphofunctional variation explained by geographical variations represented by ecoregions, independently of phylogeny, with partial CPO (using phylogeny as a covariable) also in CANOCO 4.5 (ter Braak and Šmilauer 2002). We assigned each locality to an ecoregion using the biogeographical scheme of Olson et al. (2001) in ArcView 3.3[®] (ESRI 2002). A recent example of this methodology can be seen in Morales and Giannini (2010, 2013). The same tests were performed to analyze associations between size (centroid size), phylogeny, and geographical variation.

To study the association between shape and diet, we characterized the diet type of each species with approximate percentages of vertebrates, invertebrates, and plant material consumed. Information about diet was obtained from the relevant literature (e.g., Medina-Vogel et al. 1998; Delibes et al. 2003; Zapata et al. 2005; Donadio et al. 2004; Ibarra et al. 2009; Medina et al. 2009; Valenzuela et al. 2013). A similar approach was used by Goswami (2006). We then performed Canonical Correspondence Analysis (CCA) between diet categories and shape (Procrustes coordinates) and CPO, to explore the interaction of diet and shape taking into account the group phylogeny. These analyses were performed with the software R 2.15.3 (R Development Core Team 2013) and CANOCO 4.5 (ter Braak and Šmilauer 2002).

Finally, we calculated the Clark-Evans Index (CEI) to evaluate the aggregation pattern of data points in size (Cs), shape (PCA), and shape plus size. This index measures the degree to which the distribution of individuals departs from a random distribution, with the distance from one individual to its nearest neighbor as a measure of spacing (Clark and Evans 1954). The values are restricted between 0 and 2.15,

with a clustered distribution (maximum aggregation) having values nearest to 0, a random distribution with values nearest to 1, and a systematic distribution (individuals equidistant from each other) with values near to 2.15 (Clark and Evans 1954).

Results

A Principal Component Analysis of skulls shows a clear segregation of hypercarnivorous and hypocarnivorous morphotypes. The first PC explains 64 % of total variance, and places *G. cuja*, *L. patagonicus*, and *N. vison* to the right hand side of the axis. Morphologically, these species share a reduced M1, a reduced lingual portion of the upper carnassial (P4), a longer and thinner palatal plate that is very extended beyond M1, and a longer basicranium. The opposite pattern was seen in negative values of the first axis of the PCA, where *C. chinga* is placed (see Fig. 3a). *Lontra provocax* shows an intermediate position along PC1, and does not overlap with any other species. The second axis of the PCA explains 10 % of the total variance, showing species with a more rounded zygomatic arch, a wider glenoid cavity, and a more posteriorly placed postcanine dentition towards the positive extreme, with the opposite pattern for negative values (see Fig. 3a). *Conepatus chinga* segregates from the rest by having large crushing areas on its carnassials, a shorter palatal plate, and either a rounded or straight zygomatic arch. Hypercarnivorous morphotypes include *G. cuja*, *L. patagonicus*, and *N. vison*, which shows some degree of overlap in morphospace, mainly because the importance of a greater development of shearing edges in the carnassial teeth, reduction of M1, and other morphological changes related to more positive scores on

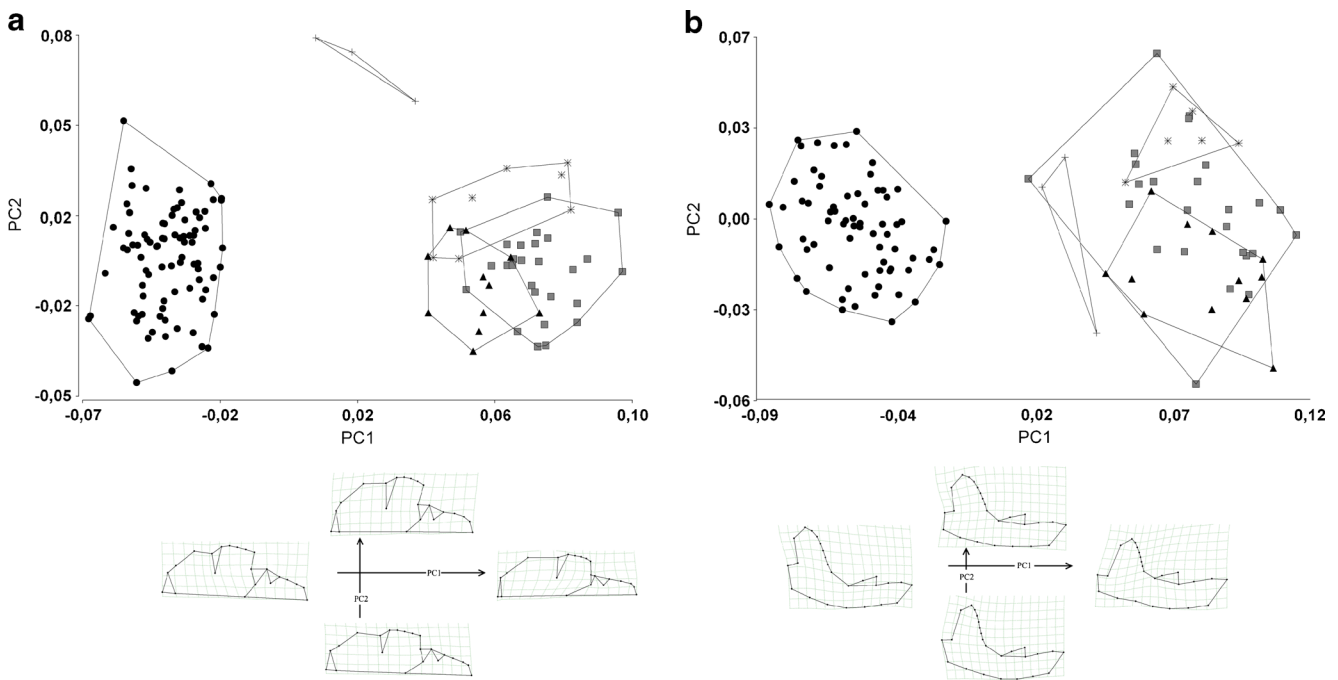


Fig. 3 Scatter-plots of PCA of skulls (**a**) and mandibles (**b**) with deformation grids. Polygons group conspecific specimens. Symbols for each species are the same as those in Fig. 1

PC1. *Lontra provocax* shows no overlap with any species, with a highly rounded and robust skull.

PC1 of mandible shape explains 67 % of the total variance, showing specimens with larger trigonids and reduced talonids, straighter coronoid processes (thinner at the tip, but wider at its base), ventrally displaced condyles, and more robust mandibular bodies (especially its anterior part) placed at the positive extreme of the axis (see Fig. 3b). The opposite pattern is observed towards negative values of PC1. PC2 explains 6 % of the total variance and shows specimens with condyles less expanded posteriorly, coronoid processes inclined posteriorly, and straighter and more robust mandibular bodies for the most positive values, with the opposite pattern towards negative values (see Fig. 3b). Similar to the skulls, *C. chinga* segregates from the rest mainly because the importance of crushing surfaces on its inferior carnassials, while some overlap is seen in more hypercarnivorous morphotypes, especially *G. cuja*, *L. patagonicus*, and *N. vison*. *Lontra provocax* shows a similar pattern to that of the cranial PCA, occupying an intermediate position in morphospace, but overlapping in this case, with *G. cuja*. *Lyncodon patagonicus* and *N. vison* are separated along PC2, but they occur within the range of mandibular variation in *G. cuja*.

In the CVA of the skulls, the first CV explained 81 % of the variance. Specimens aligned towards higher positive values showed higher shearing edges in carnassials, reduced M1s, longer palatal plates, and longer basicrania, while opposite

patterns were seen for negative values (Fig. 4a). CV2 explained almost 8 % of the variance, clearly segregating specimens that have more anterior postcanine dentitions, more posterior paracondylar processes, slightly wider palatal plates, and wider basicrania (Fig. 4a). The first two CVs clearly separated four morphotypes: *C. chinga*, *L. provocax*, *N. vison*, and another that included *G. cuja* and *L. patagonicus* with some overlap. However, significant differences in Procrustes distances among all species pairs were observed (Table 1).

The CVA of mandibles showed that CV1 explained 90 % of the total variance; specimens with relatively large talonids and reduced trigonids in m1, and shorter and more posteriorly inclined coronoid processes had higher positive values (Fig. 4b). CV2 explained only 5 % of the variance, separating specimens with more posterior postcanine dentitions and more slender mandibular bodies, which had higher positive values (Fig. 4b). As with the cranial CVA, the same four morphotypes were identified and significant differences in Procrustes distances among all species pairs were observed (Table not shown).

Analysis of skull centroid measurements showed significant differences ($P < 0.01$) between all species pairs, except between *C. chinga*-*N. vison* (Table 2). Results of mandible size analyses were the same as those for skulls, and are not shown.

Partial CPO of shape shows that only a minor percentage of variation (1 %) was explained by geographical patterns, with

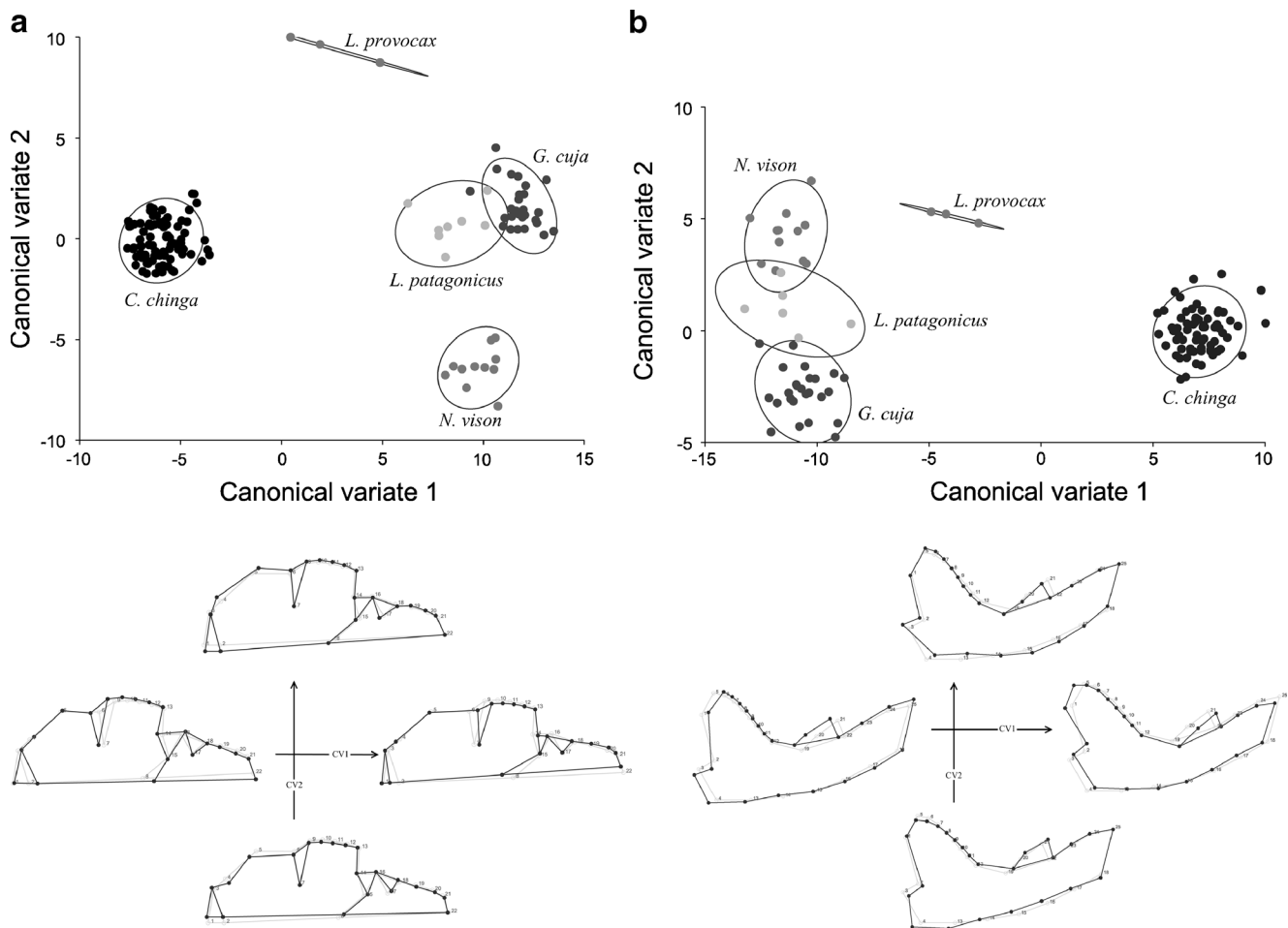


Fig. 4 CVA of skulls (**a**) and mandibles (**b**) with deformation grids. Species names are indicated in the graph. Ellipses represent probability of assignment to a group of 0.9

Patagonian Steppe (sensu Olson et al. 2001) as the only ecoregion with $P < 0.01$. CPO (shape of skulls and phylogeny independent of geographical patterns) shows that most of variation (61 %) was explained by three nodes, with $P < 0.01$. Node 2 separates mustelids from mephitids (*C. chinga*, see

Table 1 Procrustes distances (A) and P -values (B) of Procrustes distances among groups from permutation test of skulls

	<i>C. chinga</i>	<i>G. cuja</i>	<i>L. provocax</i>	<i>L. patagonicus</i>
A				
<i>G. cuja</i>	0.1027			
<i>L. provocax</i>	0.1005	0.1037		
<i>L. patagonicus</i>	0.0962	0.0463	0.0962	
<i>N. vison</i>	0.0905	0.0435	0.108	0.494
B				
<i>G. cuja</i>	<.0001			
<i>L. provocax</i>	<.0001	<.0001		
<i>L. patagonicus</i>	<.0001	<.0001	0.0058	
<i>N. vison</i>	<.0001	<.0001	0.0031	<.0001

Online Resource 2) and explains 54.6 % of the variance. Nodes 3 (Lutrinae + Ictonychinae) and 4 (Ictonychinae) explain only 2.5 % and 3.6 % of the variance, respectively (see Online Resource 2). CPO of shape and phylogeny alone shows 67 % of morphological shape variation explained by historical factors, with the same three nodes (of above) with similar percentages of explained variance.

Partial CPO shows that 10 % of size variation was explained by geographical patterns, with Chilean Matorral and Low Monte as the only ecoregions with $P < 0.01$. CPO (size and phylogeny independent of geographical patterns) shows that 27.4 % was explained by two nodes. Nodes 4 (Ictonychinae) and 3 (Lutrinae + Ictonychinae) explain 17.5 % and 9.9 % of the total variance, respectively. CPO of size and phylogeny alone shows that 48 % of size variation was explained by historical factors, with the same two nodes (of above) with similar percentages of explained variance.

As expected, we found significant association between shape and diet in CCA, with skull shape explaining 67 % of the variation in diet. The first linear combination of variables relates to vertebrate feeders in its positive coefficients, and

Table 2 *P*-values of *t*-test with Bonferroni correction for centroid size among groups

	<i>C. chinga</i>	<i>G. cuja</i>	<i>L. provocax</i>	<i>L. patagonicus</i>
<i>G. cuja</i>	<.001	–	–	
<i>L. provocax</i>	<.001	<.001	–	–
<i>L. patagonicus</i>	<.001	<.001	<.001	–
<i>N. vison</i>	1	<.001	<.001	<.001

invertebrates and plant material in its negative coefficients (Online Resource 3). The second linear combination relates to vertebrates and plant material in its positive scores, and invertebrates in its negative scores, while the third linear combination had negative coefficients for the three feeding categories. CPO of shape-diet independent of phylogeny shows very low values of association (2 %), with vertebrates as the only feeding category statistically significant ($P < 0.01$). Both for CPO and CCA mandibular analyses were highly similar to those obtained for skulls and are not shown.

The Clark Evans Index for skulls shows a distribution of points in size as randomly arranged ($CE = 0.037$, $P < 0.3986$), while shape and shape-size show a systematic arrangement ($CE = 1.68$, $P < 0.0079$, and $CE = 1.87$, $P < 0.0014$, respectively). For mandibles, size was also random ($CE = 0.04$, $P < 0.2689$), while shape and shape-size combinations have a non-significant systematic pattern ($CE = 1.73$, $P < 0.066$, and $CE = 1.92$, $P < 0.056$, respectively).

Discussion

Mammalian carnivorans are often assumed to be “keystone” species in top-down control of ecosystems (Palomares and Caro 1999). When ecologically similar species are found in sympatry, we expect a shift in size and/or morphological characters (Jones 1997), in order to minimize competition. Character displacement and character release have been extensively discussed in the literature and these concepts do not need to be reviewed here (see Dayan et al. 1989b; Jones 1997; Dayan and Simberloff 1998, 2005; Palomares and Caro 1999). Except for *N. vison*, *L. provocax* is separated from the other studied species by its semi-aquatic habits. Studying competitive processes between *L. provocax* and *N. vison* in Argentine Patagonia, Fasola et al. (2009) found no divergence in prey type between these now sympatric species, although *L. provocax* had a more specialized diet and showed some differences in habitat use (human signs and crustacean abundance). More recently, Valenzuela et al. (2012) identified trophic segregation as one of the main processes that allowed coexistence between the same two species in Tierra del Fuego, Argentina. Our results seem to be in accordance with the latter.

Based on the relative position of each species in morphospace generated by PCA and CVA, we show that considerable morphological differences between these species are evident (Procrustes differences between these two were the largest among all studied species, see Table 2), with *L. provocax* having large crushing surfaces on its carnassials and extended postcarnassial molars, which are typical of “hypocarnivorous” species that specialize in breaking hard food, such as mollusc shells. On the other hand, *N. vison* proved to be more closely related to “hypercarnivorous” species of this guild, with small talonids and well-developed shearing edges on their carnassials, which are typical of vertebrate flesh-eaters. If we assume that morphology reflects ecological adaptations (Wainright 1991), exploitative competition between *L. provocax* and *N. vison* would be unlikely to occur. Several studies have pointed to the preference of *L. provocax* for eating crustaceans (particularly the genus *Aegla* and *Samastacus*) and fishes of less than 100 mm in total length (Chehébar et al. 1984; Medina-Vogel 1998; Sielfeld and Castilla 1999; Fasola et al. 2009), while *N. vison* tends to feed on mammals, birds, fishes, and crustaceans, depending on their availability (Porro and Chehébar 1995; Fasola et al. 2009; Ibarra et al. 2009; Valenzuela et al. 2012). Our results also showed significant differences among the sizes of the crania of the studied carnivorans, with the mean size of *L. provocax* almost twice that of *N. vison* (see Table 2). However, as *N. vison* is an introduced species in southern South America since the middle of the 20th century (Pagnoni et al. 1986), we must take into account that the consequences of introduced species go well beyond competitive processes, including alteration of productivity and decomposition cycles, the wide spread of pathogens and diseases, and predation, also habitat transformation, amongst several others (see Vitousek et al. 1997; Mack et al. 2000; Olden et al. 2004; Novillo and Ojeda 2008).

Neovison vison shows a variable overlap in PCA with the two native species, *L. patagonicus* and *G. cuja*, although this overlap was not seen in CVA (which is expected, given the maximization of shape differences in this method) and significant values of Procrustes distances among these groups were observed. The American mink is often described as a semi-aquatic generalist carnivore, which may feed as much on aquatic prey as on terrestrial mammals and birds (see Valenzuela et al. 2013). Therefore, distributional separation at the habitat level may be occurring, given that, although *G. cuja* may occur in a wide range of habitats from open areas to near water habitats, its feet do not seem appropriate for swimming (Yensen and Tarifa 2003) and *L. patagonicus* seems to inhabit cold, dry areas (Prevosti and Pardiñas 2001; Schiaffini et al. 2013b). The three species have similar body plans, with long, tubular, and thin shapes (Larivière 1999; Yensen and Tarifa 2003; Prevosti et al. 2009), which allow them to go inside burrows occupied by different prey species. Although *N. vison* is often thought as a predator of aquatic prey (i.e., fish and

crustaceans), its diet seems to reflect the actual availability of food items. In this respect, Ibarra et al. (2009) showed that in Cape Horn (Chile), its diet mainly comprised small mammals, while Valenzuela et al. (2013) showed that native rodents were an important component of its diet in Tierra del Fuego (Argentina). In order to demonstrate an absence of competition between these species, a detailed distribution study of *N. vison* is needed, evaluating possible areas of syntopy (sensu Rivas 1964) with these two native species.

Galictis cuja and *L. patagonicus* are the most closely related species of the guild, according to Sato et al. (2012). Both of them belong to a “hypercarnivorous” morphotype in this guild, with strong zygomatic arches, long palatal plates, and large trigonids with reduced postcarnassial dentition, which are specializations for eating vertebrate flesh. These species are largely sympatric and syntopic (sensu Rivas 1964) in a few localities (see Fig. 1). The diet of *G. cuja* was studied by Delibes et al. (2003) and Zapata et al. (2005), who found small mammals were the main food item (particularly rodents and lagomorphs). Another study performed with the lesser grison in Uruguay identified it as responsible for the local extinction of a population of *Cavia magna* Ximenez, 1980 (Kraus and Rödel 2004). Data on the diet of *L. patagonicus* are anecdotal, but the species is supposed to feed primarily on fossorial rodents such as *Ctenomys* Blainville, 1826, and *Microcavia* Gervais and Ameghino, 1880 (Prevosti et al. 2009 and references therein). In addition, ectoparasites typical of *Ctenomys* were found on a skin of *L. patagonicus* (Castro and Cicchino 1986). Significant differences in size were observed between these species (see Table 2), with the lesser grison being much larger than the Patagonian weasel. Size differences may result in avoidance of competition for limited resources (Dayan and Simberloff 1998), with larger predators taking a larger range of sizes of prey (Schoener 1969). So, trophic segregation in size may be occurring between these species, with *G. cuja* preying on a variety of rodents and introduced lagomorphs, and *L. patagonicus* specializing in preying on fossorial rodents such as *Ctenomys* and/or *Microcavia*. However, future ecological research at different geographical scales for *G. cuja* and dietary analyses for the enigmatic *L. patagonicus* are needed to test this hypothesis.

Both PCA and CVA shows *C. chinga* as a morphotype that does not overlap with any of the other species in this guild. It displays a large intraspecific variability in size and in some shape features (straight or rounded zygomatic arches, a more slender or robust skull, and a variable mandibular body length). Zapata et al. (2008) found some overlap between *C. chinga* and *Lycalopex griseus* (Gray, 1837) (= *Pseudalopex griseus*), owing mainly to similar crushing areas on their carnassials, indicating that some trophic overlap (i.e., feeding on invertebrates) may exist. Future research should also take into account the possible relationship with other small

mammals present in the southern cone of South America, like the xenarthran *Zaedyus pichiy* (Desmarest, 1804). The diet of this small (≈ 1 kg) armadillo has been studied in Mendoza, Argentina by Superina et al. (2009), who found beetles, ants, and plant material as the main food types consumed. Remarkably, some of these same food items are eaten by *C. chinga* (see Donadio et al. 2004; Medina et al. 2009).

Combining shape and size analyses and the Clark Evans tests, it is clear that there is a good separation between species, which could reflect reduced ecological overlap and competition (Dayan et al. 1990). These results also indicate that there could be some competition between *G. cuja*, *L. patagonicus*, and *N. vison*, but this is minimal or absent between them and the other two taxa (and between these two as well). Additionally, habitat separates *L. provocax* from other species, with the exception of *N. vison*. The CPO showed that a large proportion of shape is related to cladogenetic events, especially at node 2, which separates these mustelids from *C. chinga*. This particular event seems to have occurred ≈ 30 Mya (Sato et al. 2012) and is responsible for 60 % of the actual morphological variance. The two most similar species (*G. cuja* and *L. patagonicus*) belong to the same subfamily (Ictonychinae) and the basal split appears to have occurred only ≈ 2.9 Ma, after the Panamanian bridge was completed (Sato et al. 2012). These analyses indicate that morphological and dietary differences between these taxa are related to historical factors (i.e., processes related to cladogenesis) and not necessarily to ecological processes, but that they help to structure the guild by minimizing ecological overlap. In this sense, historical factors seem also responsible for a certain degree of size differences, particularly between *G. cuja* and *L. patagonicus*, which may imply that only a small amount of ecological difference between these two species could be the result of ecological processes. Furthermore, only a small (10 %), but significant, variation in size has been explained by geographical patterns alone. This relationship may include the effects of temperature and rainfall on primary production (McNab 2010). The mismatch between the absence of ecological overlap between *L. provocax* and *N. vison*, which was expected from cranial/mandibular shape and size versus the dietary overlap viewed in some localities (Fasola et al. 2009), can also be explained by historical factors, where *N. vison* retains a more hypercarnivorous morph inherited from its ancestral form (maybe due to an evolutionary constraint, Losos 2011), but has adapted into a more generalized diet.

Future lines of research based on ecological studies and the comparison between morphological and size differences between target species, and between syntopic and non-syntopic areas, could shed more light on the interaction between shape/size and trophic segregation at an ecological scale.

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