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REVIEW

# Native, exotic, and livestock prey: assessment of puma *Puma concolor* diet in South American temperate region

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**Abstract**
Understanding the food habits of mammalian carnivores is crucial for the comprehension of the role of apex-predators in maintaining healthy ecosystems. The puma is currently the most widespread top predator and the carnivore most frequently involved in conflicts with humans in the Americas. We analyzed puma diet in the South American temperate region, a vast area largely modified by humans, to assess the importance of native prey with respect to livestock and exotic species. We reviewed 18 studies published between 1991 and 2020 to which we added 19 feces of puma from a rangeland area of central Argentina. "Undetermined small rodent," plains vizcacha, European hare, and wild boar were the most frequent species in the small area of the Argentinean Espinal. In the southern temperate region, exotic (European hare and wild boar) and native species (guanaco and armadillos) were the most frequent wild prey species, while sheep was the most frequent livestock followed by cattle. Exotic species had a greater frequency of occurrence than native and livestock species. Livestock frequency of occurrence was greater inside protected areas than outside. These findings reveal that, although the puma is considered in this large area as conflictive, wild prey (exotic and native) are its main food sources. Given the potentially crucial role exotic species can play in the ecosystem, understanding the role of pumas in controlling their populations is a challenge for future research.

**Keywords** Cougar · Exotic prey · Human-carnivore conflict · Livestock · Mountain lion · Patagonia · Predation

## Introduction

After centuries of persecution (Stolzenburg 2008), large carnivores are increasingly recovering their social reputation thanks to the recognition of their major role in maintaining ecosystem processes and biodiversity (Terborgh et al. 1999; Ray et al. 2005). As apex predators, large carnivores have important impacts on densities and behavior of both prey and mesopredator species, generating top-down effects across ecosystem trophic webs (Terborgh and Estes 2013; Ripple et al. 2014). However, in human-modified landscapes, carnivore persecution and alteration on prey abundances (du Toit et al. 2017) can drastically affect the potential of apex predators in regulating ecosystem dynamics (Newsome and Ripple 2015; Kuijper et al. 2016). Mostly due to the global habitat loss and fragmentation, as well as the human conflict provoked by livestock predation, large carnivores are among the world's most threatened species (Treves and Karanth 2003; Ripple et al. 2014). Describing large carnivores' food habits contributes to understand their ecological importance in preserving ecosystem health, and simultaneously provides valuable information on the status of wild prey populations. This is particularly relevant in rangelands which are the most extensive land-use globally (Lund 2007; Briske 2017).

The puma *Puma concolor* is one of the most widely distributed and highly adaptable large carnivores in the Americas (Elbroch and Quigley 2019). Although puma diet predominantly relies on large prey (70 to 165 kg; Carbone et al. 1999), this felid feeds on diverse terrestrial and semiterrestrial vertebrates (Ruth and Murphy 2009). Because of predation on

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livestock, the puma is broadly considered a "conflictive" species (Inskip and Zimmermann 2009; Murphy and Macdonald 2010), even if less than 10% of feces composition is typically attributable to domestic prey (Ruth and Murphy 2009).

Puma food habits have been largely studied across its geographic distribution (e.g., Rau and Jiménez 2002; Novack et al. 2005; Elbroch and Wittmer 2013; Gómez-Ortiz et al. 2015). North American studies reported diets mainly based on large prey, particularly cervids, such as elk *Cervus elaphus* (Husseman et al. 2003), mule deer *Odocoileus hemionus* (Smith et al. 2016), and white-tailed deer *Odocoileus virginianus* (Cassaigne et al. 2016). In Central and South America, where large prey is less common, puma diet comprises a greater variety of species, spanning from large (guanaco *Lama guanicoe*, Pia 2013; Vicugna *Vicugna vicugna*, Pacheco et al. 2004, collared peccary *Tayassu tajaco*, Rueda et al. 2013; common rhea *Rhea americana*, Pessino et al. 2001) to medium and small prey (e.g., Pudu *Pudu puda*, Rau et al. 1991; nine-banded armadillo *Dasypus novemcinctus*, Gómez-Ortiz et al. 2015). Because of their generalistic feeding behavior, pumas also readily prey on exotic species, including the European hare *Lepus europaeus*, wild boar *Sus scrofa*, and European rabbit *Oryctolagus cuniculus* (Buenavista and Palomares 2018).

Temperate zones are the most extensively human-altered regions in the world: in these areas, many species have been entirely extirpated, while others are constrained to fragmented and highly modified remnants of natural ecosystems (Baldi et al. 2006; Wilcove et al. 1986). The distribution range of *P. concolor* covers, approximately, 1,837,630.675 km$^2$ of the South American temperate region (from latitudes greater than 35° S). In this region, the nearly continuous puma's distribution (with the exception of Tierra del Fuego province; Nielsen et al. 2015) overlaps with scarcely preserved landscapes. Only 13.1% of this large territory is under legal protection, where poorly connected protected areas are concentrated, mainly, along the Andean range. Large native ungulates (guanaco, Pampas deer *Ozotoceros bezoarticus*, Patagonian huemul *Hippocamelus bisulcus*), in this region, have been heavily hunted and/or still compete with livestock herds (Baldi et al. 2001; Dellafiore et al. 2003; Flueck and Smith-Flueck 2006; FAO 2010), as well as with several introduced mammal species (Buenavista and Palomares 2018).

In this study, we analyzed puma diet in a rangeland area of the Espinal ecoregion and reviewed literature available from South American temperate regions. Given native large prey depletion, increasing exotic prey availability (Buenavista and Palomares 2018), and widespread puma-livestock conflict (Kissling et al. 2009; Llanos et al. 2014; Llanos and Travaini 2020; Guerisoli et al. 2017; Iriarte-Walton et al. 2016), we expected that in this region: (1) puma diet would primarily rely on exotic prey (Buenavista and Palomares 2018), and (2) livestock would represents a common food source. Finally, since protected areas (PAs) main goal is long-term wildlife conservation (Day et al. 2012), we also expected that (3) pumas would preferentially prey on wild species inside PAs.

## Materials and methods

### The Espinal ecoregion, samples collection, and processing

This ecoregion is mostly flat, and natural vegetation is mainly characterized by xerophytic species (dominated by species of the genus *Prosopis*), which depending on their relative density create different habitats (woodlands, grasslands with shrubs, and grasslands; Distel 2016; Oyarzabal et al. 2018). However, because of agriculture and ranching expansion, natural habitats suffered heavy human modification (Nanni et al. 2020), especially in the southern portion of this region (Patagones and Villarino counties, Buenos Aires Province; Appendix 1). Here, extensive livestock (cattle *Bos taurus* and sheep *Ovis aries*) breeding is one of the major sources of economic income (SENASA 2015).

A previous camera-trapping study (sampling effort: 10,621 camera-trap days) completed in this area, revealed that pumas occurred in 35 out of 86 sampling sites (Guerisoli et al. 2019). Mammals species presented in this region include the guanaco, Patagonian mara *Dolichotis patagonum*, plains vizcacha *Lagostomus maximus*, armadillos (large hairy armadillo *Chaetophractus villosus*, screaming hairy armadillo *C. vellerosus*, and pichi *Zaedyus pichiy*), and small rodents (mainly Caviidae and Cricetidae families) (Arturi et al. 2005). In this area are also present large to medium-size bird species, particularly the common rhea and partridges (such as the elegant crested tinamou *Eudromia elegans*, spotted nothura *Nothura maculosa*, Darwin's nothura *Nothura darwinii*, brushland tinamou *Nothoprocta cinerascens*, and red-winged tinamou *Rhynchotus rufescens*). Because of human persecution and livestock presence, guanacos and plains vizcachas are rare and spatially localized, whereas introduced species (wild boars and European hares) are relatively common (Arturi et al. 2005). In this study area, it was estimated, trough line transects, low densities of wild prey (e.g., range: 0.1–1.3 ind/km$^2$; Olla 2016) compared to livestock densities (22.9 sheep/km$^2$ and 54.2 cattle/km$^2$; SENASA 2015). Thus, we suggest that livestock largely outweighed wild prey in most of the study area.

Between 2014 and 2016, puma feces were collected in a rangeland area in the southern part of the Espinal (Latitude 38.4–4° S, Longitude 63.4–62° W; Appendix 1, Fig. 1). We completed 15 transects stratified per habitat (woodlands, grasslands, and grassland with shrubs). Each transect included 2–3 operators and a scat-detection dog (Border collie breed trained by Matías Piedrabuena; "Got Scat?" Project, https://www.facebook.com/gotscat/). The dog was specifically

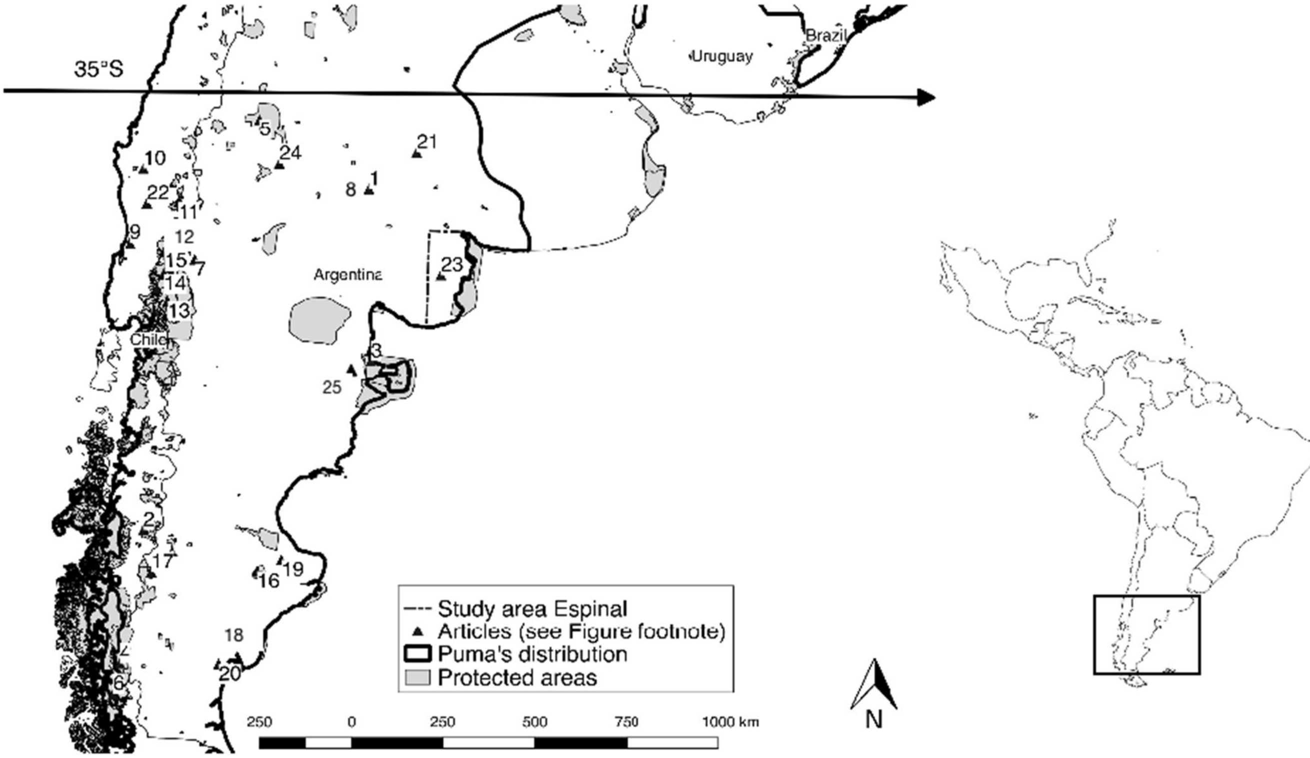


**Fig. 1** Location of the study areas of puma (*Puma concolor*) diet reviewed literature from the South American temperate region (area below the 35° S parallel; black line). Black lines show puma distribution range (IUCN, Nielsen et al. 2015) and gray polygons represent the PAs (WDPA). Map also includes the study area of our fieldwork-based data (#23). 1: Branch et al. 1996, 2: Elbroch and Wittmer 2013, 3: Fernández and Baldi 2014, 4: Ferreyra et al. 2010, 5: Gelin et al. 2017, 6: Iriarte et el. 1991, 7: Novaro et al. 2000, 8: Pessino et al. 2001, 9: Rau and Jiménez 2002, 10: Rau and Jiménez 2002, 11: Rau and Jiménez 2002, 12: Rau and Jiménez 2002, 13: Rau and Jiménez 2002, 14: Rau et al. 1991, 15: Skewes et al. 2012, 16: Zanón-Martínez et al. 2012, 17: Zanón-Martínez et al. 2012, 18: Zanón-Martínez et al. 2012, 19: Zanón-Martínez et al. 2012, 20: Zanón-Martínez et al. 2012, 21: Sarasola et al. 2016 and Zanón Martínez et al. 2016, 22: Zúñiga et al. 2005 and Zúñiga and Pedreros 2014, 23: our study, 24: Palacios, 25: LLanos and Travaini 2020

trained to search the scent of puma feces' and to avoid the scents of the other carnivores present in the area (Geoffroy's cat *Leopardus geoffroyi*, Pampas cat *Leopardus colocolo*, Pampas fox *Lycalopex gymnocercus*, and dog *Canis lupus domesticus*). The length of each transect ranged from 1 to 7 km and averaged 3.9 km. Each transect was surveyed five to six times, achieving a total sampling effort of approximately 350 km. The identification of the pumas feces was based on the color, shape, texture, diameter, and macroscopic content (Yáñez et al. 1986). For each sample, we recorded the geographic coordinates. The feces were stored in paper bags, at room temperature, until further analyses.

To assess the feces content, we followed the point-frame method, described in Ciucci et al. (2004). Feces were first volume-weighted, then soaked in water and soap for 24–48 h, disaggregated, and then thoroughly filtrated (0.7–0.5 mesh size) under running water. Once the samples were dried, we mixed and distributed each feces component in a 10 × 10 cm grid. Then, through a systematic sampling, we extracted 100 items (hairs) from each sample for identification. All the solid materials (e.g., bones, claws), of each feces, were identified through macroscopic identification (Pearson 1995; Rau and Jiménez 2002). To avoid inter-observer bias, only one trained observer (MMG) performed the items identification. Prey remains were identified to the lowest possible taxonomical level. The hairs were identified using an optical microscope and following the cuticle and medullar patterns for local mammals described in both Chehébar and Martín (1989) and Bonzano and Dellafiore (2018).

The prey consumption was expressed as the frequency of occurrence (FO; number of feces containing a given item divided by the total number of feces) and the relative biomass (B) for each detected item (i). For biomass estimates, we used the Ackerman's linear correction factor (Ackerman et al. 1984; $B_i$) applying the following equations:

$$Bi = Fo_i * (0.035 * BM_i + 1.98) \quad \text{for prey} > 2 \text{ kg}$$

$$Bi = FOi * BM_i \quad \text{for prey} < 2 \text{ kg}$$

where Bi = prey biomass (kg)/feces and $BM_i$ = body weight of prey (item "*i*") in kg.

The Ackerman's correction factor (Ackerman et al. 1984) was designed especially for pumas, and we believe that, although it is a linear factor, it is the most suitable way to estimate prey biomass consumption in the temperate southern region. We expressed $B_i$ as percentage, dividing the contribution of each item by the sum of all items contributions to the total biomass consumed. Since $B_i$ estimation depends strongly on the prey body weight used for calculation, we identified livestock most predated age classes based on information obtained through interviews to ranchers and direct observations of puma killing sites from the field (see Guerisoli et al. 2017 for more details). We then used the average adult body weight for *O. aries* and the average under 12 months old calves and foals weights for *B. taurus* and *Equus caballus*, respectively. Finally, we extracted the remaining prey weights from different sources, specified in Table 1.

To understand if the sample size was representative of prey species presented in the area we applied a species accumulation curve (Foster et al. 2010) using the *specaccum* function of the *Vegan* R package (RStudio Team 2020).

**Puma diet in South American temperate region: search criteria and data extraction for literature review** South American temperate region is a large area (1,570,150 km$^2$) characterized by temperate climate (Köppen-Geiger climate classification; Beck et al. 2018) and comprehending portions of both Argentine and Chilean territories below the 35° S parallel (Fig. 1). We performed a systematic search of puma food habits studies with Scopus (Scopus 2019) and Google Scholar (Google 2019), using "key words" (e.g., *Puma concolor* + diet + feces). We included all the articles published until the year 2020 and located in the South American temperate region. The results obtained in the Espinal study area were also included in the review.

From each literature, we extracted the frequency of occurrence (FO) of each item (expressed as the number of feces containing a given item divided by the total number of feces), and when authors did not reported this value (e.g., Gelin et al. 2017), we calculated it based on the samples size and the number of occurrences of each item. We considered only the FO because provides an objective information about how often a given item is eaten (Zabala and Zuberogoitia 2003), and represents the most cited parameter in carnivore diet studies (e.g., Díaz-Ruiz et al. 2013; Soe et al. 2017). We used an overall FO values for multiple year sampling of a same study area (e.g., Zúñiga et al. 2005 and Zúñiga and Pedreros 2014; Appendix 2), while when a study presented multiple study areas results, we consider an FO per area (e.g., Rau and Jiménez 2002; Appendix 2). We discarded the "*P. concolor*" item since we assumed that could be derived from a grooming behavior.

**Definition of prey categories and conservation areas for comparative analyses** Following Scognamillo et al. (2003), we categorized prey in three body size groups: small (< 1 kg), medium (1–15 kg), and large (> 15 kg). Additionally, we categorized food items into native, exotic (wild boar and European hare) and livestock (e.g., cattle, sheep). Because livestock breeding is not completely absent inside PAs, for both Argentina (e.g., APN 2019) and Chile (Praus et al. 2011), and following the initial hypothesis of a difference in puma feeding behavior depending on the conservation status of each study area, we categorized the researches inside or outside the PAs. Finally, we checked for significant differences between the mean FO of each prey category (prey size and exotic, native, livestock), and between inside and outside

**Table 1** *Puma concolor* diet composition in a rangeland area of the Espinal ecoregion in Argentina based on 19 feces collected between 2014 and 2016. FO, frequency of occurrence (%; in parenthesis the number of each item detections); Bi, prey biomass (%) estimates based on Ackerman et al. (1984); W, prey weights obtained from: [a]Jones et al. (2009), PanTHERIA database (*L. guanicoe* was replaced with the data available for *L. glama*); [b]mean weight for "small prey" (Scognamillo et al. 2003); [c]field-collected records; [d]mean weight of small birds (e.g., yellow cardinal *Gubernatrix cristata*) and medium-sized birds (e.g., elegant crested tinamou) present in the study area from BirdLife

| | Large > 15 kg | | | | Medium 1–15 kg | | | | Small < 1 kg | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Item | W | FO | Bi | Item | W | FO | Bi | Item | W | FO | Bi |
| Native | *Lama guanicoe* | 78.3[a] | 15.8 (3) | 13.6 | *Lagostomus maximus* | 4.6[a] | 47.3 (9) | 18.4 | *Cricetidae* | 0.5 | 5.3 (1) | 0.4 |
| | | | | | *Zaedyus pichi* | 1.4[a] | 5.3 (1) | 1.3 | Cavy (*Microcavia australis* or *Galea musteloides*) | 0.3[a] | 5.3 (1) | 0.3 |
| | | | | | *Unidentified armadillo* | 1.4[a] | 10.5 (2) | 2.6 | *Ctenomys* sp. | 0.4[a] | 5.3 (1) | 0.3 |
| | | | | | | | | | Unidentified small rodents | 0.5[b] | 63.2 (12) | 6.3 |
| | | | | | | | | | Unidentified Medium/small birds | 0.4[d] | 15.8 (3) | 1.2 |
| Exotic | *Sus scrofa* | 84.4[a] | 31.5 (6) | 28.4 | *Lepus europaeus* | 3.8[a] | 31.5 (6) | 12.1 | | | | |
| Livestock | *Bos taurus* | 100[c] | 5.3 (1) | 5.3 | | | | | | | | |
| | *Ovis aries* | 65[c] | 5.3 (1) | 4 | | | | | | | | |
| | *Equus caballus* | 100[c] | 5.3 (1) | 5.3 | | | | | | | | |

PAs, performing a $Z$-test. To overcome potential bias due to variation in sample size, we generated 95% confidence intervals (CI) around each prey category value through non-simultaneous bootstrap considering 1000 iterations with the library *boot* of RStudio Team (Manly 2018).

## Results

**Diet composition in a rangeland area of southernmost Espinal ecoregion** We collected 19 puma feces (corresponding to an encounter rate of 0.05 feces/km) with a feces mean volume of 45.8 (± 35 SD) ml. We detected 2.5 (± 1.4) food items per feces, and identified 14 different food items (11 to the species and/or genus level and three unidentified categories [armadillo, small rodents, and medium/small birds]; Table 1). The species accumulation curve did not reach a *plateau*, indicating that the number of samples was insufficient for a complete description of puma diet in this area (Appendix 3). The mean body weight of ingested prey was 31.5 (±42.6, range: 0.4–100) kg. The most frequent prey species were "undetermined small rodent," followed by plains vizcacha, European hare, and wild boar (Table 1). Although we detected livestock in approximately 16% of the samples, each single livestock species had a FO slightly more than 5% (Table 1). The $B_i$ estimates showed a greater relative biomass contribution for large and medium prey than small prey, indicating that only four species (plains vizcacha, European hare, guanaco, and wild boar) exceeded 10% of biomass consumed (Table 1). Overall, native species represented the group with the largest ingested biomass, followed in descending order, by exotics and livestock (Table 1).

**Literature reviewed and puma diet description in South American temperate region** We reviewed 18 papers containing relevant information on puma diet for the region, published between 1991 and 2020, and corresponding to 25 different study areas (Fig. 1; Appendix 2). Two papers described puma food habits in more than one study area, two involved the same area and the remaining were one-site surveys (Appendix 2). Counting also our field-based study, we found more information from Argentina ($n_{pub} = 12$, $n_{studyareas} = 16$) than Chile ($n_{pub} = 6$, $n_{studyareas} = 10$; Fig. 1). Most studies characterized puma diet through feces analysis, one through kill site inspections, and one with both stomach and intestine content (Appendix 2).

Hare (*L. europaeus*; 88.4%, $n = 23$, of the 26 study areas), guanaco (53.8%, $n = 14$ study areas), armadillos (*Z. pichi* and *C. villosus*; 50%, $n = 13$ study areas), and wild boar (30.7%, $n = 8$ study areas) were the most recorded wild species in puma diet (Table 2). Among livestock, sheep was the most common item (40% of the study areas), followed by cattle (Table 2). The FO varied across study areas, with the lowest FO for wild boar (0.1%) to the greatest for guanaco (83.5%) and hares (86%; Table 2). Although plains vizcacha and pudu were found in only 4 and 6 study areas, respectively, they presented high values of FO (12.8–87.1% and 8.3–64%, respectively; Table 2). The ranges of the FO of the other species are presented in Table 2.

**Prey categories and conservation areas** Large prey category was composed mainly by livestock and native species, while medium and small prey categories was largely represented by native prey (Table 2). Medium prey tended to present a higher mean FO (24.8%, SD = ± 27%, $n = 71$) than large prey (19%, SD = ± 21.9%, $n = 51$). However, we did not detect any significant difference between their values (Z = − 1.6, $p = 0.09$), and CIs widely overlapped (Fig. 2, a1). Large and medium prey categories presented greater mean FO values than small prey (8.9%, SD = ± 10.3%, $n = 48$; large vs small: $Z = 2.9$, $p < 0.05$; medium vs small: $Z = 4.9$, $p < 0.05$) and their CIs did not present overlaps (Fig. 2, a2).

Exotic species (34%, SD = ± 26.9%, $n = 37$) presented a higher mean FO than native (15.7%, SD = ± 20.3%, $n = 107$; Z = 3.9, $p < 0.05$) and livestock species (8.3%, SD = ± 9.1%, $n = 25$; Z = 5.5, $p < 0.05$). While the mean FO of native preys was higher than livestock species (Z = − 2.7, $p < 0.05$). The CIs showed very small overlap between livestock and native species (Fig. 2, a2).

Nineteen study areas were located inside PAs, while 7 were located in private lands (outside PAs). Sampled studies PAs were mainly concentrated along the Andes Mountains, varying in surface extension, from 0.89 to 21,689 km$^2$ (Fig. 1). Puma diet tended to rely less on native species inside PAs (mean FO = 14.5%, SD = ± 20.1%, $n = 84$) than outside (mean FO = 19.9%, SD = ± 21%, $n = 23$), even if this difference was not significant (Z = − 0.8, $p = 0.4$). The higher mean FO in puma diet of exotic species inside PAs (35.9%, SD = ± 30.2%, $n = 25$) than outside (29.9%, SD = ± 18.6%, $n = 12$) was also not significant ($Z = 0.8$, $p = 0.4$). Finally, livestock mean FO inside PAs (9.1%, SD = ± 10%, $n = 19$) was significantly ($Z = 2$, $p < 0.05$) greater than outside (5.4%, SD = ± 4.7%, $n = 6$). Regardless of the similar CIs extents between protected and non-protected areas, exotic species CIs clearly showed that the FO values were greater than native and domestic species inside PAs and did not overlap with these categories (Fig. 2, B). On the other hand, CIs largely overlapped between exotic and native species outside PAs, while domestic species had smaller FOs and their CIs did not overlap with any of the other categories (Fig. 2, B).

## Discussion

### Diet composition in a rangeland area of southern Espinal ecoregion

**Sample size** Under this productive context, where pumas are protagonist of an intense conflict with ranchers because of

**Table 2** Diet composition of *Puma concolor* in South American temperate region (data from 18 reviewed papers and field-based results from this study). Study areas where the prey size category has been detected (N), and frequency of occurrence (FO; mean, min-max) are shown per prey group size (top row) and main category (leftmost column). Mean values for those species which were found in one study area are not presented

| | Large > 15 kg | | | Medium 1–15 kg | | | Small < 1 kg | | |
|---|---|---|---|---|---|---|---|---|---|
| | Species | N | FO (%; mean, min-max) | Species | N | FO (%; mean, min-max) | Species | N | FO (%; mean, min-max) |
| Native | *Lama guanicoe* | 14 | 41.09, 0.4–83.3 | *Pudu pudu* | 6 | 36.73, 8.3–64 | *Abrothrix longipilis* | 3 | 4.62, 1.5–10 |
| | *Hippocamelus bisulcus* | 1 | 1.5 | *Chaetophractus villosus* | 6 | 9.88, 0.5–39.2 | *Loxodontomys micropus* | 3 | 13.41, 0.2–20 |
| | *Rhea americana* | 1 | 1 | *Lagostomus maximus* | 4 | 46.77, 12.8–87.1 | *Abrothrix olivaceus* | 2 | 6.53, 3–10 |
| | *Rhea pennata* | 2 | 3.99, 1.4–6.5 | *Dolichotis patagonum* | 4 | 9.3, 0.3–22.2 | *Oligoryzomys longicaudatus* | 2 | 5.76, 1.5–10 |
| | | | | *Myocastor coypus* | 2 | 17.05, 16.6–17.4 | *Graomys griseoflavus* | 2 | 22.4, 1.2–43.6 |
| | | | | *Lycalopex griseus* | 1 | 2.9 | *Eligmodontia typus* | 1 | 15.4 |
| | | | | *Galea musteloides* | 3 | 2.93, 0.5–4.8 | *Ctenomys mendocinus* | 2 | 3.65, 2.8–4.5 |
| | | | | *Conepatus chinga* | 3 | 2.76, 1.2–4.2 | *Akodon molinae* | 1 | 1.2 |
| | | | | *Lycalopex gymnocercus* | 2 | 11.6, 2–21.2 | *Akodon iniscatus* | 1 | 2.8 |
| | | | | *Leopardus geoffroyi* | 3 | 6.22, 2.6–12 | *Reithrodon auritus* | 1 | 1.2 |
| | | | | *Galictis cuja* | 1 | 0.5 | *Thylamys pallidior* | 1 | 1.2 |
| | | | | *Pseudalopex culpaeus* | 2 | 0.73, 0.2–1.2 | *Reithrodon physodes* | 1 | 0.4 |
| | | | | *Conepatus humboldtii* | 1 | 1.5 | *Phyllotis darwini* | 1 | 0.2 |
| | | | | *Conepatus* sp. | 1 | 2.5 | *Histiotus* sp. | 1 | 5.7 |
| | | | | *Felidae* | 2 | 1.85, 0.7–3 | *Ctenomys* sp. | 3 | 8.98, 5.3–13.3 |
| | | | | *Leopardus* sp. | 1 | 1.2 | *Cricetidae* | 3 | 17.4, 5.3–26 |
| | | | | *Chloephaga picta* | 2 | 3.43, 0.4–6.4 | *Microcavia australis/Galea musteloide* | 3 | 8.17, 2.5–15.4 |
| | | | | *Cygnus melancoryphus* | 1 | 33.3 | *Dromiciops gliroides* | 1 | 33.3 |
| | | | | *Spheniscus magellanicus* | 1 | 38.2 | *Zaedyus pichi* | 7 | 8.31, 1.1–15.4 |
| | | | | *Tupinanbis* sp. | 1 | 1 | *Zenaida auriculata* | 2 | 40.9, 40.9–56 |
| | | | | | | | *Anas* sp. | 1 | 1.2 |
| % and N of native prey per size category | 35.3%, *n* = 18 | | | 64.4%, *n* = 47 | | | 95.5%, *n* = 42 | | |
| Exotic | *Sus scrofa* | 8 | 20.34, 0.1–37.1 | *Lepus europaeus* | 23 | 44.65, 1.1–86.0 | *Mus musculus* | 1 | 1.2 |
| | *Cervus elaphus* | 3 | 11.13, 0.5–31.2 | *Oryctolagus cuniculus* | 1 | 31.4 | *Rattus rattus* | 1 | 3.6 |
| % and N of exotic prey per size category | 25.5%, *n* = 11 | | | 32.8%, *n* = 24 | | | 4.5%, *n* = 2 | | |
| Livestock | *Ovis aries* | 10 | 11.72, 0.4–35.3 | *Gallus domesticus* | 1 | 2.3 | | | |
| | *Bos taurus* | 6 | 3.69, 0.4–9.1 | *Anser anser* | 1 | 2.4 | | | |
| | *Equus caballus* | 2 | 9.55, 5.2–13.9 | | | | | | |
| | *Capra hircus* | 4 | 6.66, 0.5–11.5 | | | | | | |
| % of livestock per size category | 43.1%, *n* = 22 | | | 2.7%, *n* = 2 | | | NA | | |

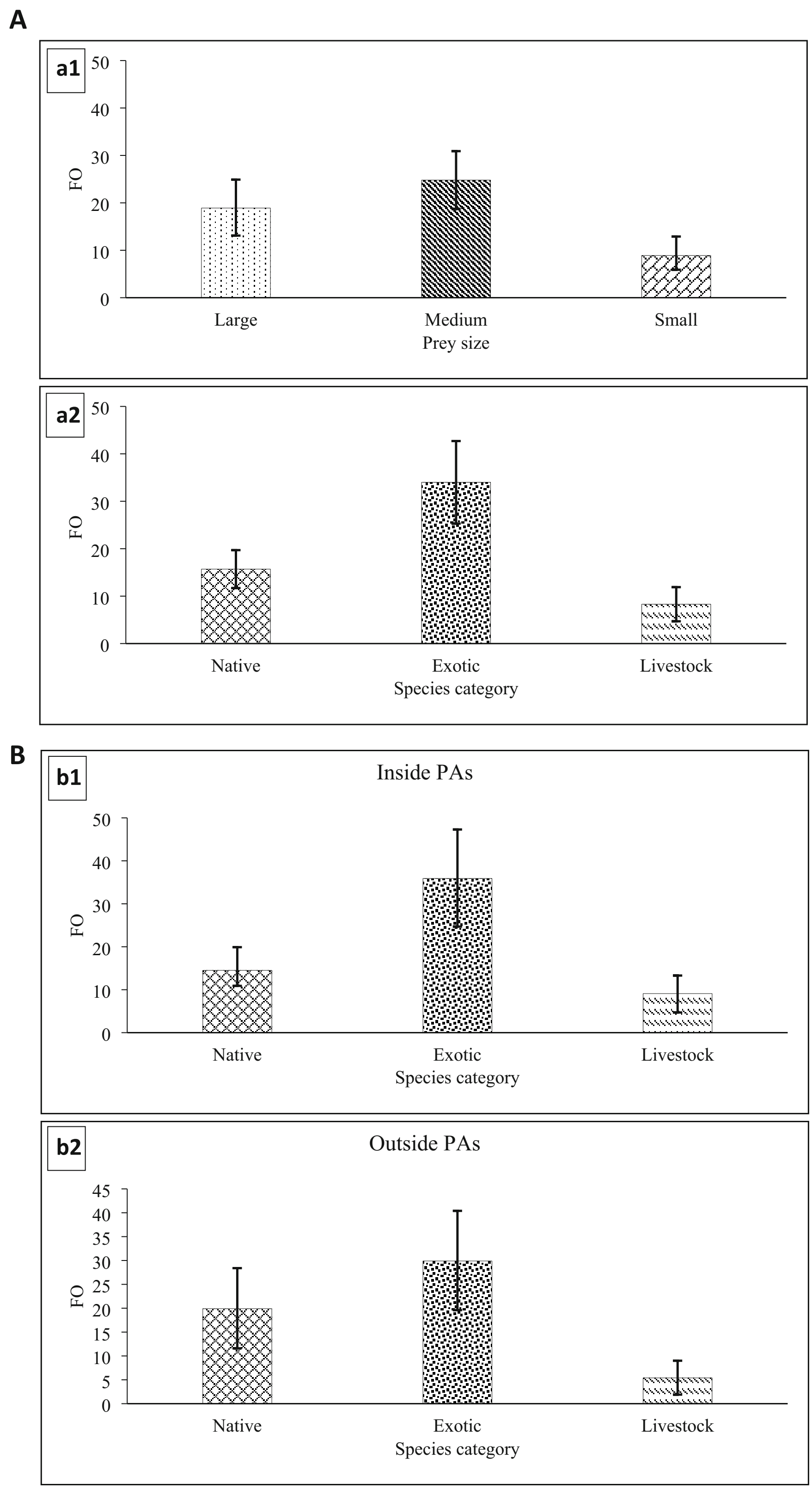


**Fig. 2** Mean frequency of occurrence (FO, %) and 95% confidence intervals (non-simultaneous bootstrap considering 1000 iterations) of the prey categories reported by puma diet studies (18 reviewed papers and field-based results from this study) from South America temperate region.. $A_1$: size (large, medium, small), $A_2$: species (native, exotic, livestock), $B_1$ and $B_2$ compare the same categories than $A_2$ for inside and outside protected areas (PAs), respectively

livestock predation (Guerisoli et al. 2017), this feline was mainly concentrated in the consumption of two exotic preys: the European hare and wild boar. Surprisingly, livestock species were underrepresented in the samples, while native prey (plains vizcacha and "undetermined small rodents") were also among the first items in its diet. We acknowledge that the sample size ($n = 19$) was low. A small encounter rate of feces can be associated, for example, to weather conditions or to specific behaviors of felids (e.g., burying their feces; Reed et al. 2011). Considering the sampling effort completed and the use of a scat detection dog, we think that perhaps a low density of pumas, along with an intense human persecution of this species, could have affected the encounter rate. Although puma density has never been estimated for this study area, Gallo et al. (n.d.) estimated, for an area with similar habitat, 0.23 pumas/100km$^2$, a density lower than 0.30 individuals/100km$^2$ estimated for an area in northeast Argentina where this felid is strongly persecuted (Paviolo et al. 2009).

The species accumulation curve did not reach a *plateau*, indicating that the sample size was insufficient to completely describe puma diet. This was further supported by the fact that we did not detect common rhea remains through samples processing, despite the discovering of a puma kill-site on this species during fieldwork activities (Guerisoli personal observation). However, and in spite of the rarity and restricted distribution of some species, we detected two (*L. guanicoe* and *S. scrofa*) of the three (*L. guanicoe*, *S. scrofa*, and *Rhea americana*) large wild prey present in the area and that were already reported for puma diet in other studies (Skewes et al. 2012; Gelin et al. 2017). Still, further studies are needed to reliably describe large prey relevance for this felid diet in this area.

**Puma diet in South American temperate region** Our results suggest that the European hare is the most detected wild prey in the southern temperate region, followed by guanaco and wild boar. In accordance with Buenavista and Palomares (2018), in more than half of the studies, exotic species were the most recorded items, showing greater FO than native prey. Additionally, the exotic wild boar and European hare are also among the five species with the greatest FO in puma feces in this vast region. Medium preys were the most represented size category in puma diet. This is consistent with Monroy-Vilchis et al. (2009), who indicated that pumas typically tend to prey on large mammals, whereas, at the southern limits of its distribution, they mainly feed on medium-sized prey. However, it has to be underlined that native species, with a size similar to the European hare (i.e., Patagonian mara and plains vizcacha), were present only in a small number of areas (Patagonian mara, $n = 4$ study areas, plains vizcacha, $n = 4$). Thus, for this size category (medium prey), our findings support the hypothesis proposed by Novaro et al. (2000) for northern Patagonia, where native species could have largely been replaced by exotic species. The same authors reported high-density estimates ($45.4 \pm 5$ individuals/km$^2$; Novaro et al. 2000) of European hare in unprotected areas. Consistently, this species has been found to represent an important food resource also for many mesopredators of the South American temperate region (i.e., culpeo *Lycalopex culpaeus*, chilla *Lycalopex griseus*, Geoffroy's cat, and Pampas cat; Buenavista and Palomares 2018).

Among large prey, guanacos were the most recorded item ($n = 14$, 78.2% of the study areas). Due to hunting pressure, natural grassland deterioration, caused mainly by the sheep overgrazing (Golluscio et al. 1998), and direct interspecific competition with livestock, this native camelid has experienced an abrupt decline since the 1800s (Baldi et al. 2010). Although recent findings reported an increase of guanaco populations in the Argentine Patagonia (Gavuzzo et al. 2015), and most of the studies reviewed found this item, guanacos could be facing negative consequences due to wild boar density, which has been estimated to be around 35 km$^2$/year in the Argentinean Patagonia (Pescador et al. 2009).

Regarding livestock, sheep were among all items, the third most common prey, but in general, the FO of livestock species was smaller than those of wild prey species. The puma is considered a conflictive species in the temperate region of South America, due to livestock predation (e.g., Novaro et al. 2000; Llanos et al. 2014; Guerisoli et al. 2017; Lucherini et al. 2018; Guerisoli et al. 2020). In this region, sheep prevalence in the diet, compared with cattle and goats, likely relates to the predominant abundance of this domestic species in Patagonia (FAO 2010), where additionally, pumas suffer heavy retaliation killing (Llanos et al. 2014). Food habits description represents an important tool/resource of information to complement data on pumas predation on livestock, which is recommended to be assessed also, with ranch monitoring and kill site surveys (Guerisoli et al. 2020), since livestock items can originate from opportunistic scavenging (Bauer et al. 2005).

**Protected areas** Internationally recognized as one of the 37 biogeographic regions in the world which preserved its wild conditions (Mittermeier et al. 2003), the Patagonian ecoregion identifies almost the entire South American temperate region. Here, while most of the National Parks are located in proximity of the Andean mountain range (WDPA 2019), their number in eastern Patagonia (corresponding to the great *plateau* extending between the Andean mountain range towards the Atlantic coast; Steffen 1944) is almost null (WDPA 2019). Thus, the network of PAs in this territory is poorly conserving the most characteristic and widespread landscapes of the region: the Patagonian steppe. Most of the literature we reviewed involved protected areas, and yet 40% of them included *O. aries* in puma diet. Additionally, the FO of both exotic and livestock species were greater inside than outside PAs. More studies are needed to better understand the importance of conservation efforts in preserving this top predator's ecological role inside PAs, as well as to more properly describe its trophic ecology outside PAs.

Based on the potential crucial role covered by exotic species as food resource, puma key role in prey populations control (Elbroch and Wittmer 2013; Barry et al. 2019) could be especially relevant for constraining the ongoing geographic expansion and population size increase of these species in the South American temperate region. Exotic species, including wild boar and European hare, can be responsible of serious conservation and management issues, including spread of diseases to livestock and people, vehicle collisions, reduction in native species abundance and richness (Jaksic 1998; Massei and Genov 2014). Thus, by predating on them, pumas not only control their populations, but also could provide an additional service by avoiding or reducing indirect issues that these species presence frequently cause (Barry et al. 2019). Conversely, exotic species could represent alternative prey to livestock, particularly when native species are less abundant, thus attenuating puma-human conflict. However, further research is required to properly understand predator-prey interactions in this vast region, where ecosystems and their vertebrate communities have been extensively altered by human action.

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**Data availability** We provide supplementary material.

## Compliance with ethical standards

**Conflict of interest** Not applicable.

**Ethics approval** Not applicable.

**Consent to participate** Not applicable.

**Consent for publication** Yes, we consent.

**Code availability** Not applicable.

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