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REVIEW

The role of exotic mammals in the diet of native carnivores from South America

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ABSTRACT

1. A better understanding of the effects of exotic species is fundamental for ecosystem management, given that biological invasions are major agents of change affecting native biodiversity worldwide. However, exotic species can also have positive effects on native communities, for instance by providing additional food sources.

2. We reviewed dietary studies in the scientific literature published between 1980 and 2016 in order to examine the role of exotic mammals in the diets of 42 terrestrial species of the mammalian order Carnivora from South America. We recorded information about species' characteristics and analysed the ways in which they relate to exotic mammal consumption.

3. We found 62 references in which 11 carnivores from four families were reported to consume exotic mammals. Using only dietary studies in which the frequency of occurrence of each prey item was presented, we compiled 152 cases from 56 papers.

4. The frequency of occurrence of exotic mammals in the diet of South American carnivores reached on average 21%. The more common prey–carnivore interactions occurred with exotic lagomorphs, while exotic ungulates were less frequently consumed and were only preyed upon by pumas *Puma concolor*. Consumers with mainly carnivorous habits consumed exotic mammals more frequently than frugivorous or omnivorous species.

5. The carnivore species and the location of the study area influenced the frequency of occurrence of exotic mammals in the diets described. Certain carnivores, including the puma, culpeo fox *Lycalopex culpaeus*, Pampas fox *Lycalopex gimnocercus*, lesser grison *Galictis cuja* and Molina's hog-nosed skunk *Conepatus chinga*, consumed more exotic mammals than average, and the occurrence of exotic mammals was the highest in the diets of carnivores in the southwestern regions of South America.

6. Exotic mammals in South America can create new food web interactions in the native carnivore community and can serve as an important food resource for some native species. This is particularly true in human-transformed landscapes, where native prey populations have declined. Thus, it is important to consider the role of exotic mammals in the conservation of native carnivore populations.

INTRODUCTION

The redistribution of species by humans has occurred and continues to occur worldwide. The globalisation process promotes a large flux of plants and animals between continents, producing an unprecedented increase in the number of species involved in the processes of biological invasion around the world (Meyerson & Mooney 2007, Hulme

2009). Biological invasion is one of the main drivers of global environmental change and the loss of native biodiversity, preceded only by habitat destruction (Chapin et al. 2000, Sala et al. 2000). Further, anthropogenic changes in the landscape can increase the vulnerability of native biological communities and the availability of resources on which exotic species thrive (Chapin et al. 2000). The impact of human activities on land use and land cover changes may alter the composition of the native prey community and the relative abundance of prey for carnivore species (Foley et al. 2005, Rodriguez 2006). Therefore, trophic interactions between the prey assemblage and species with carnivorous feeding habits can be strongly influenced by the ecological extinction of the native prey species (Novaro et al. 2000) and by the availability of newly introduced species (Chapin et al. 1998, Berger 2008). Besides, there is evidence that omnivorous mammals may be able to increase their density and their geographical range through an increase in the variability of their diet favoured by new food resources, such as exotic species, in a wide range of anthropogenic landscapes (Fedriani et al. 2001, Rodriguez 2006, Clavero et al. 2008, Tablado et al. 2010, Dijkstra et al. 2013, Barrientos et al. 2014).

The role of exotic species as a trophic resource is interesting because, although there is a rapidly growing number of publications on the importance of species introduction (Vitousek et al. 1996, Ballari et al. 2016), there has been insufficient investigation into the effects of exotic species on the carnivore community (Rodriguez et al. 2005). Moreover, trophic niche modification in native carnivores after the introduction of exotic prey is poorly understood (Barber et al. 2008).

Exotic mammals in South America

According to Novillo and Ojeda (2008), exotic mammals in South America account for about 20% of the world's mammal introductions, and most of these occur in the southern cone of this region (Ballari et al. 2016). There is substantial information available on the status of introduced mammalian species in Chile (Jaksić 1998, Jaksić et al. 2002, Iriarte et al. 2005) and Argentina (Jackson 1988, Lizarralde et al. 2004, Bonino & Soriguer 2009), where most of the region is occupied by exotic species. Moreover, these areas have been highly modified by humans and the abundance of native prey populations fluctuates significantly (Novaro et al. 2000). In other countries, such as Uruguay and Peru, information about exotic mammals is often scarce, inaccurate or only reported in the grey literature (Pereira-Garbero et al. 2013, Zeballos et al. 2012).

Among exotic mammals in South America, the highest spread rates (10–20 km/year) are reached in exotic lagomorph species: the European hare *Lepus europaeus* and European rabbit *Oryctolagus cuniculus* (Grigera & Rapoport 1983, Alves & Hackländer 2008). These species occupy very dissimilar environments throughout the southern region and continue to expand their ranges, invading new areas quickly (Jaksić et al. 2002). The rabbit and the wild boar *Sus scrofa*, also widespread in South America (Jaksić et al. 2002, Bonino & Soriguer 2009, Barrios-García & Ballari 2012), are included on the list of "100 of the world's worst invasive alien species" (Lowe et al. 2000). They provide good examples of the disastrous consequences that can result from the introduction of exotic species in different ecosystems in South America (Long 2003, Barrios-García & Ballari 2012). The European hare is catalogued as a pest in Argentina and Chile, where it is known to cause economic and ecological damage (Bonino et al. 2010), and has also been reported damaging crops and orchards in Bolivia and Peru (Zeballos et al. 2012). The geographic range of the European hare includes practically all of Argentina, Chile and Uruguay, southeastern Peru, southwestern Bolivia, southeastern Paraguay, and the central part of southern Brazil (Bonino et al. 2010). The European rabbit is present in Tierra del Fuego and Patagonia in southern Chile and Argentina, in the west-central Argentinian provinces of Mendoza and Neuquén, and in central Chile (Bonino & Soriguer 2009). The wild boar is an exotic species in Chile, Argentina, Brazil and Uruguay (Salvador 2012), and other ungulates such as the red deer *Cervus elaphus* have been introduced in Argentina, Chile and Uruguay (Flueck 2010). However, an accurate and current map of the distribution of these ungulates in South America is not available.

Other mammalian species, such as the common hippopotamus *Hippopotamus amphibius* in Colombia (Valderrama 2012), the American mink *Neovison vison,* the American beaver *Castor canadensis* and the common muskrat *Ondatra zibethicus* (Merino et al. 2009, Guichón et al. 2016) are among the exotic species in South America. However, their distribution or abundance is less extensive on this continent (Novillo & Ojeda 2008). Exotic mammal populations are sometimes restricted to hunting reserves (Merino et al. 2009). This occurs with populations of some exotic ungulates, such as the white-tailed deer *Odocoileus virginianus,* Père David's deer *Elaphurus davidianus,* the Himalayan tahr *Hemitragus jemlahicus,* the European bison *Bison bonasus,* the alpine chamois *Rupicapra rupicapra,* the European mouflon *Ovis aries musimon,* and the alpine ibex *Capra ibex* (Navas 1987, Bonino 1995).

In this study, we review the evidence for the consumption of exotic mammals by terrestrial species of the mammalian order Carnivora that are native to South America.

Specifically, we ask the following questions: (1) Which Carnivora from South America prey on exotic mammals? (2) How important are exotic mammals in the diets of these carnivores? (3) What are the characteristics of the carnivore species that prey on exotic mammals? (4) What characteristics of the study area and the carnivore species affect the frequency of occurrence of exotic mammals in the diets of the carnivores?

METHODS

Bibliographic search

The terrestrial species belonging to the mammalian order Carnivora in South America comprise 52 species in eight families (Anonymous 2016a). In our study, we did not include 10 species of otter, seal, elephant seal, and sea lion, due to their aquatic habits and because they are not frequent predators of terrestrial mammals. Therefore, we assessed 42 species of six families of carnivores with terrestrial habits. We reviewed the scientific literature on the diets of these 42 species of terrestrial carnivore by searching for keywords in both English and Spanish in Google Scholar, Web of Science and SCOPUS. We used the same keywords for each search ("scientific binomial name" AND "diet" OR "feeding habits"). We also included searches for variant scientific names of carnivore species (e.g. genus "*Lycalopex*" and "*Pseudalopex*" for the South American foxes). We examined the dietary studies and compiled those that included information about the consumption of exotic mammals by native carnivores. We did not consider in our compilation domestic species or livestock consumed by South American carnivores. We only selected those studies where carnivores fed upon wild exotic mammal species. We included in our analysis only medium and large exotic mammals consumed, and excluded small exotic mammals, such as rodents, because small prey items were frequently not identified at the species level in the dietary studies (Martínez-Gutiérrez 2017). When the consumption of more than one exotic species was reported in the same study, we selected the consumption of each exotic mammal species as a separate case, and did the same for studies that examined more than one carnivore species consuming exotic mammals in the same study area. Although including all cases reporting exotic mammal consumption by different species from a single study could decrease the independence of some data points, it allowed us to explore responses of native carnivores to a broader range of exotic species. Each study evaluating more than one area was treated as a different case, and data on seasonal dietary changes in the same study area were averaged for the same year. We selected papers, dissertations, theses and book chapters, including all publications up to July 2016. Finally, within the references of dietary studies reporting the consumption of exotic mammals by terrestrial carnivores, we summarised the frequency of occurrence (occurrence of a particular prey item over the total) of exotic mammals in each carnivore's diet if it was reported in the study, with the objective of analysing the importance of exotic mammals in the diet for each carnivore using a standardised method (Appendix S1).

Data analysis

To analyse the characteristics of the carnivore species that consumed exotic mammals, we only considered the two exotic lagomorph species as exotic prey, due to the lack of reliable range maps for other exotic mammals in South America. We considered that a carnivore species is potentially able to prey on the exotic lagomorph if its range overlaps with the known range of the lagomorph (Appendix S2). Geographic ranges of both carnivores and lagomorphs were obtained from the International Union for Conservation of Nature's (IUCN) Red List database (Anonymous 2016a). The carnivore characteristics considered for analyses were family (Canidae, Felidae, Mephitidae, Mustelidae, and Procyonidae), body size (large: >20 kg, medium: 5–20 kg and small: <5 kg), general habitat use (generalist, open habitat, and closed habitat), and activity pattern (nocturnal or diurnal). Not all members of the mammalian order Carnivora have strictly carnivorous feeding habits. Thus, we also included the different feeding habits (carnivorous, frugivorous, and omnivorous; Appendix S2; adapted from Medel & Jaksić 1988, Nowell & Jackson 1996, Sunquist & Sunquist 2002, Sillero-Zubiri et al. 2004) as characteristics in our analyses. Because the data set for carnivore species with geographic ranges overlapping with those of exotic lagomorphs was small ($n = 19$), we used a Monte Carlo simulation based on 2000 replicates with the "chisq.test" function in R software v. 3.3.1 (Anonymous 2016b) to test for any significant trends. For each data point in the papers with information about the frequency of occurrence of exotic mammals in the diet, we determined those factors that could influence consumption. We fitted generalised linear models, using quasibinomial distribution to account for over-dispersion for proportion data and logit link, using the "glm" function in R. We modelled the frequency of occurrence of each exotic item in the carnivore diet as a dependent variable and the carnivore species, exotic species consumed, the number of faeces sampled for the dietary study, protection category (protected area or unprotected area), latitude, and longitude of the study area as predictors.

RESULTS

Bibliographic search

In all, we found 62 publications in which trophic interactions between native carnivores from South America and exotic mammals were documented (Appendix S1). We found that 11 carnivore species from four different families, of the 42 terrestrial carnivore species considered in this study, fed upon exotic mammals. The carnivore assemblage that preyed on exotic mammals included five felid species (puma *Puma concolor*, Geoffroy's cat *Leopardus geoffroyi*, colocolo *Leopardus colocolo*, kodkod *Leopardus guigna*, and Andean mountain cat *Leopardus jacobitus*), three canid species (culpeo fox *Lycalopex culpaeus*, South American grey fox *Lycalopex griseus* and Pampas fox *Lycalopex gimnocercus*), two species in the Mephitidae family (Molina's hog-nosed skunk *Conepatus chinga* and Humboldt's hog-nosed skunk *Conepatus humboldtii*), and one mustelid species (lesser grison *Galictis cuja*). Of the exotic mammals consumed as prey items by native carnivores, we found two lagomorph species, the European hare (n = 108) and the European rabbit (n = 32), and two ungulate species, the wild boar (n = 16) and the red deer (n = 4; Appendix S1). We found information about the occurrence of European hare consumption by 10 out of the 11 carnivore species preying on exotic mammals. Four carnivores were felids: puma (n = 46 cases), Geoffroy's cat (n = 10 cases), colocolo (n = 4 cases) and Andean mountain cat (n = 1); three were canids: culpeo (n = 19 cases), South American grey fox (n = 11 cases) and Pampas fox (n = 5 cases); two were skunks: Molina's hog-nosed skunk (n = 5 cases) and Humboldt's hog-nosed skunk (n = 2 cases); and one was a mustelid: lesser grison (n = 4 cases). However, only five carnivore species preyed on European rabbits: culpeo fox (n = 15), South American grey fox (n = 7), kodkod (n = 3), lesser grison (n = 5), and rarely, the puma (n = 2). On the other hand, exotic ungulate species were consumed in South America only by the puma (n = 20 cases). The ungulate that was most frequently preyed upon was the wild boar (n = 16), followed by the red deer (n = 4; Appendix S1).

Importance of exotic mammals

Taking into account only the dietary studies in which information on the frequency of occurrence of exotic mammals in the diet was reported, we found 56 publications, providing a total of 152 cases or data points (Table 1; Appendix S1). In 103 cases (67%), the prey species consumed was the European hare, in 30 cases the European rabbit (20%), in 16 cases the wild boar (10%) and in four cases the red deer (2%). The carnivore species with the highest number of reported cases of consumption of exotic mammals expressed as frequency of occurrence, was the puma (n = 66), followed by the culpeo fox (n = 30) and the South American grey fox (n = 17; Table 1). The other carnivore species each accounted for 1–9 data points of exotic mammal consumption (Table 1).

The frequency of occurrence of exotic mammals in the carnivores' diet was on average 21% (n = 152 cases; Table 1). The puma, culpeo fox and lesser grison exceeded this occurrence of exotic mammals in their diets, and the South American grey fox was very close; the lowest frequency of occurrence of exotic mammals in the diet was found in both skunk species and in the Andean mountain cat (Table 1). In more than half of the cases analysed

Table 1. Importance of exotic mammals in the diets of native carnivores: frequency of occurrence of exotic mammals in the diets of 11 South American carnivores for which predation was detected in a bibliographical search from 1980 to July 2016

Carnivore species	Study cases	Frequency of occurrence		Exotic mammal consumed
		Mean	Range	
Puma	66	23.4	0.1–100	European hare, European rabbit, wild boar, red deer
Colocolo	4	7.4	2–10.2	European hare
Geoffroy's cat	9	14.6	1.5–57.4	European hare
Kodkod	3	11.7	6.9–20	European rabbit
Andean mountain cat	1	3.5	3.5	European hare
Culpeo fox	30	26.0	0.4–90	European hare, European rabbit
American grey fox	17	11.0	0.6–41.4	European hare, European rabbit
Pampas fox	5	18.4	3.8–34	European hare
Molina's hog-nosed skunk	6	4.8	0.6–15.7	European hare
Humboldt's hog-nosed skunk	2	3.7	0.6–6.8	European hare
Lesser grison	9	39.4	18.9–96.8	European hare, European rabbit
Total	**152**	**21.0**	**0.1–100**	European hare, European rabbit, wild boar, red deer

Table 2. Results of the generalised linear model with quasibinomial error estimating the influence on frequency of occurrence of exotic mammals consumed by native carnivores in South America, according to carnivore species, exotic mammal consumed, number of faeces analysed in the dietary study, latitude, longitude, and protection category of the study area

Factors	Levels	Estimate	Standard error	*t* value	Pr(>|t|)
Carnivore species	Molina's hog-nosed skunk	–16.70000	4.03400	–4.140	0.00006 ***
	Humboldt's hog-nosed skunk	0.34200	1.89100	0.181	0.85676
	Lesser grison	2.49600	0.92330	2.703	0.00776 **
	Colocolo	1.16200	1.22300	0.950	0.34365
	Geoffroy's cat	1.90000	0.97570	1.948	0.05354†
	Kodkod	1.19400	1.21800	0.981	0.32844
	Andean mountain cat	0.51120	2.58100	0.198	0.84328
	Culpeo	2.14400	0.90040	2.381	0.01868 *
	South American grey fox	0.92590	0.94400	0.981	0.32843
	Pampas fox	3.31700	1.06400	3.116	0.00224 **
	Puma	2.50300	0.88740	2.821	0.00552 **
Exotic mammal prey	Wild boar	0.84780	2.87700	0.295	0.76865
	Red deer	–0.24040	3.05500	–0.079	0.93741
	European hare	1.45600	2.86400	0.508	0.61200
	European rabbit	1.21700	2.87900	0.423	0.67309
	Number of faeces analysed	0.00047	0.00069	0.677	0.49944
	Latitude of study area	–0.04694	0.01587	–2.957	0.00367 **
	Longitude of study area	–0.15340	0.03416	–4.492	0.00002 ***
Protection category	Protected area	–0.18770	1.55500	–0.121	0.90416
	Non-protected area	–0.92920	1.55100	–0.599	0.55009

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, †$P < 0.1$.

(n = 80), the authors of the dietary studies indicated the importance of exotic items in the carnivores' diets. In one-third of the case studies (n = 53), exotic mammals exceeded 21% of the frequency of occurrence in the diet, and lagomorph species were consumed in almost all cases when this rate exceeded 21% (n = 49).

Characteristics of carnivores consuming exotic mammals

Among the 42 terrestrial carnivore species from South America, only 19 species have geographic ranges overlapping with those of exotic lagomorphs. Of these 19 species, we found evidence that 11 consume one or both species of exotic lagomorphs. The largest of these carnivores by far is the puma (35 – 105 kg, Sunquist & Sunquist 2002), followed by the culpeo fox (6–12 kg, Sillero-Zubiri et al. 2004). The other cats and canids are intermediate (2–8 kg) in size, and the lesser grison and skunk species are the smallest (<1–3 kg, Sunquist & Sunquist 2002). However, we did not find any relationship between carnivore species' body size and their consumption of exotic lagomorphs (X^2 = 1.497, d.f. = 2, $P > 0.05$). We did not detect significant differences among families in terms of consumption or non-consumption of exotic mammals by carnivore species (X^2 = 6.6932, d.f. = 4, $P > 0.05$). In addition, significant differences were not found relating to different activity patterns of carnivores (X^2 = 2.2491, d.f. = 1, $P > 0.05$) or in relation to the biotopes inhabited by the carnivores (X^2 = 2.9328, d.f. = 2, $P > 0.05$). Whether or not species consumed exotic mammals only varied significantly in native carnivores with different feeding habits (X^2 = 13.14, d.f. = 2, P = 0.004). Carnivore species with frugivorous habits did not consume exotic lagomorphs, while two omnivorous species consumed them and four omnivorous species did not. Nine out of 11 carnivorous species consumed exotic lagomorphs (Appendix S2).

Factors influencing the frequency of occurrence of exotic prey in the diets of native carnivores

The frequency of occurrence of exotic mammals in the diets of native carnivores was significantly related to the carnivore species, and the latitude and longitude of the study area (Table 2). Molina's hog-nosed skunk, the lesser grison, the culpeo and the Pampas fox, the puma and, marginally, Geoffroy's cat consumed exotic mammals more frequently than the other carnivore species (Tables 1 and 2). On the other hand, in the study areas in the southern and western parts of South America, the frequency of occurrence of exotic mammals in the diets of native carnivores was higher (Figure 1).

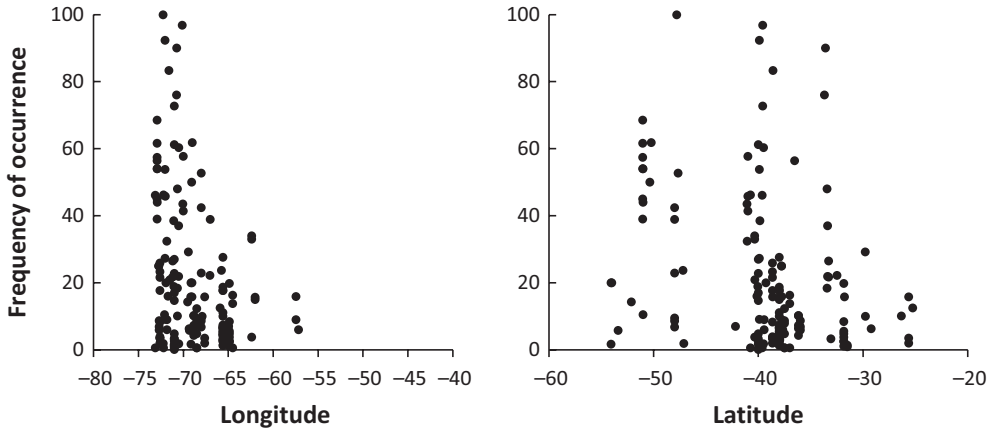

Fig. 1. Frequency of occurrence of exotic mammals in the diets of native carnivores, in relation to the latitude and longitude of the study area in South America.

DISCUSSION

This review supports the hypothesis that the adaptive response of native predators determines their use of a new prey resource (Berthon 2015). According to the optimal foraging theory, predators should choose the most profitable prey item, such as exotic species (Krebs & Davies 1993). In general, our results show that carnivore species in South America often consume exotic mammals if they are present within the geographic range of the carnivore, and that these exotic species may even make up an important proportion of the diets of native carnivores. In addition, the authors of several other studies conclude that carnivores usually change their food habits when native prey populations decline (Iriarte et al. 1991, Novaro et al. 2000), and may consume more than one exotic species if they are present in the area (Branch et al. 1996, Novaro et al. 2000, Skewes et al. 2012). Therefore, exotic mammals appear to be supplementing native prey resources, which may be the main food items for carnivores in some cases. This occurs in Argentine Patagonia, where native species, such as guanacos *Lama guanicoe* and rheas *Pterocnemia pennata*, are ecologically extinct as prey (Cunazza et al. 1995, Baldi et al. 1997, Barri et al. 2008). Thus, in this region, the carnivore assemblage, and particularly culpeos and pumas, rely primarily on exotic mammals (Novaro et al. 2000). This may explain, at least in part, why some carnivore populations have not declined, despite declines in their native prey populations, if exotic mammals have served as an alternative food source (Novaro et al. 2000, 2004, Walker et al. 2007, Zanón Martínez et al. 2016).

Carnivore species' characteristics may affect the speed with which each native carnivore species begins to consume new prey (such as an exotic mammal species). In particular, the degree to which the native carnivore is a carnivorous diet generalist or specialist may affect the prey switch (Pintor & Byers 2015). Among the five carnivore families with geographic ranges that overlap with those of exotic lagomorphs in South America, the families Canidae, Felidae, and Mephitidae include species that are opportunistic carnivores and display trophic plasticity; this facilitates their greater consumption of exotic prey (Jaksić et al. 1980, Iriarte et al. 1990, Novaro et al. 2004). The high variability in prey items found in their diets supports the existence of opportunistic predatory behaviour in these carnivore families, although mammalian species were preferred according to their occurrence (Martínez-Gutiérrez 2017). In the case of both skunk species, usually described as opportunistic omnivorous feeders and primarily insectivorous (Zapata et al. 2001, Donadio et al. 2004, Castillo et al. 2014), a low frequency of occurrence of exotic lagomorphs was evidenced in the dietary studies in which exotics were found to be consumed, suggesting that skunks only occasionally consume exotic mammals, such as vertebrate carrion (Travaini et al. 1998, Zapata et al. 2001, 2007). Procyonidae was the only carnivore family in which no species consumed exotic mammals, probably due to their arboreal lifestyle and specialised frugivorous diet (Robinson & Redford 2008).

In South America, the southwestern region includes areas where wild exotic mammals exhibit their most invasive ranges and where they are present at the highest densities (Bonino & Soriguer 2009, Bonino et al. 2010, Skewes & Jaksić 2015). This may explain why, in this region, the consumption of exotic mammals as the main food is a widespread phenomenon within the carnivore community (Novaro et al. 2000). This is well represented in the published literature (Iriarte et al. 2005, Novillo & Ojeda 2008), and all the cases found in this review were distributed in Argentina and Chile (Appendix S2).

Barbar et al. (2016) found that among native raptors and mammalian predators, some of which are carnivores, the occurrence of exotic lagomorphs in the diet is 20% in South America and Oceania. This indicates a strong trophic interaction between the native predator community and exotic prey species, given that, when lagomorphs are not present in the native predator diet, the average frequency of occurrence of the main native prey is about 24% (Barbar et al. 2016). In our review, we calculated that the average frequency of occurrence of exotic mammals in the diet of carnivores in South America was 21%. Taking only the frequency of occurrence of exotic ungulates consumed as documented in the dietary studies, the average frequency of occurrence in the diet decreases to 13%. However, it is important to consider that ungulate species represent a large biomass, and thus, this prey offers more energy than medium-sized prey species such as lagomorphs.

Due to their numbers, body size, and vulnerability, species in the order Lagomorpha are consumed by several predators worldwide, playing key ecological roles within trophic systems (Alves & Hackländer 2008). Moreover, fluctuations in their abundance have strong impacts on carnivore abundance and predation on alternative prey (Lees & Bell 2008, Delibes-Mateos et al. 2011). Even though the European hare and the European rabbit are exotic lagomorphs in South America, they may play a role similar to those of key species in the prey–predator interactions on this continent (Alves & Hackländer 2008). Throughout the literature reviewed in this study, we found that when exotic lagomorphs become established in an area, they become an important food resource for native carnivore species. This finding was consistent with those of other authors, who confirm that exotic lagomorphs account for a high percentage of the biomass consumed by native carnivores in South America (Delibes et al. 2003, Novaro et al. 2004, Barbar et al. 2016, Galende & Raffaele 2016).

Data for exotic ungulate species in South America are scarcer than those for exotic lagomorphs. Nevertheless, we considered it important to analyse their role in the carnivores' diet, especially for large carnivores. The consumption of wild boar by the puma has increased in recent decades, so that it has become an important prey item since the reduction in native prey populations (Novaro et al. 2000). In central Argentina, the population of the Argentine plain vizcacha *Lagostomus maximus* declined by 90% over a decade. This species had been the main prey for the puma, but with this decline, the wild boar became four times more frequent in diet of the puma (Branch et al. 1996). Similarly, in southern Chile, pumas doubled their consumption of wild boar between 1988 and 2004 (Skewes et al. 2012). Research in North America, where wild boar and deer species constitute the prey base for the puma, suggests that similar trends have occurred there. In Florida, wild boar became the most common prey item for pumas, and other ungulates, such as red deer, are important for pumas in other areas of North America (Ackermann et al. 1984, Iriarte et al. 1990).

Recent land-use changes in South America may lead to increased expansion of large exotic mammals, such as ungulates (Acevedo et al. 2011, Lantschner et al. 2013) that could serve as prey for threatened carnivores. This phenomenon may compensate for the decline in large carnivore species due to habitat loss and degradation in human-transformed areas, and due to poaching and strong hunting pressure on prey species (Woodroffe 2000, Ceballos & Ehrlich 2002, Dorresteijn et al. 2015). This is the case for the jaguar *Panthera onca*. It has been hypothesised that the presence of large prey, such as wild boar, could aid the recovery of jaguars in agricultural areas in Brazil (Verdade et al. 2015). Moreover, the presence of free-ranging exotic herbivore species could help to reduce conflicts between humans and large carnivore species in regions traditionally occupied by husbandry ranches, if carnivores include exotic species in their diets more frequently (Cavalcanti & Gese 2010). Nevertheless, the conflict could also be exacerbated if the presence of exotic species leads to increases in the abundance of predators, which may then threaten more livestock.

Although the introduction of exotic prey may have positive effects on carnivore populations, it may have negative impacts on native prey populations. For example, increases in predator numbers that are associated with exotic prey may produce cascading effects that would increase the impact of predation on native prey (Tablado et al. 2010), or increase the negative impact of exotic ungulate species by competition with native herbivores (Courchamp et al. 2000).

Considering both the negative and positive effects as a whole will lead to more effective management of invasive species and conservation of native carnivore populations. Moreover, the continued investigation of trophic niche modification in native carnivore species after the introduction of a new potential prey species can allow for a better understanding of the impacts of exotic mammals in native communities and ecosystems. This is particularly important in human-transformed landscapes, where food webs are altered after native prey numbers decline (Roig 1989, Cunazza et al. 1995, Baldi et al. 1997, Barri et al. 2008) and exotic species reach high densities (Jaksić et al. 2002, Barrios-García & Ballari 2012, Lantschner et al. 2013), playing an important role as trophic resources for native carnivores (Pyke et al. 1977).

Carnivore diets in South America have generally been well documented based on faecal analysis, but the identity of the carnivore species has generally not been

confirmed by genetic tests (Klare et al. 2011, Martínez-Gutiérrez et al. 2015). It is easy to confuse the faeces of different carnivore species (Farrell et al. 2000, Elbroch & Wittmer 2012). Thus, although this review indicates the number of native carnivores consuming exotic mammals, it would be interesting to consider future dietary studies, using genetic methods to confirm the carnivore species.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. References and information on dietary studies in which consumption of exotic mammals by terrestrial carnivores from South America was reported.

Appendix S2. Characteristics of the terrestrial carnivores in South America with ranges overlapping those of exotic lagomorphs (European rabbit and European hare).