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Intraguild Predation and Interspecific Killing as Structuring Forces of Carnivoran Communities in South America

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Abstract Intraguild predation (IGP) and interspecific killing (IK) have been recently acknowledged as important ecological forces that could influence community structure. Not only can carnivores influence prey community composition, they might also impact the populations of other carnivores. The goal of the current study was to assess the role of IGP and IK as significant forces influencing carnivoran assemblages in South America. To this end, we compiled the available records on 35 species of terrestrial carnivorans in the subcontinent, to investigate the potential and actual extent of IGP/IK as widespread ecological forces. We considered potential intraguild predators those having >20 % range overlap and body mass 2–5.4 times greater than that of other guild members and likely-potential intraguild predators those that, in addition, were also hypercarnivorous. The potential number of intraguild predators for those species evaluated ranged from zero to 18 (mean=5.35±SE 0.74). IGP/IK events (n=116) included 52 pairs of Neotropical carnivorans, 13 of which were killers and 25 were victims. Confirmed intraguild predator species (n=13) accounted for 37.1 % of the assemblage, nearly the same value predicted to be likely potential predators (n=14). IGP and IK were highly associated with the hypercarnivorous felids, whereas victim species were most often the omnivorous procyonids and skunks. The results indicate jaguars, pumas, and ocelots as the species most likely to have significant impact on the guild. IGP and IK are not random and reflect widespread interactions that influence carnivoran community structure in South America.

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Introduction

After the assessment of Polis et al. (1989), intraguild predation (i.e., the killing and eating behavior among potential competitors, Arim and Marquet 2004) and interspecific killing (i.e., the killing of potentially competing species without any immediate energetic gain to the predator species, Polis et al. 1989), have been afforded increasing relevance as ecological forces involved in structuring communities. Both intraguild predation (IGP) and interspecific killing (IK), the most extreme forms of interference competition, have been reported for a wide variety of animal taxa (Polis et al. 1989; Arim and Marquet 2004; Gagnon et al. 2011) and have potential effects on the ecology and evolution of the species involved (Polis et al. 1989; Polis and Holt 1992). The behavior of IGP and IK predators may not only impact the populations of other predators, but also influence the composition of prey communities by their effects on interspecific competitors and shaping the evolutionary history of the species involved (e.g., Courchamp et al. 1999; Crooks and Soulé 1999; Finke and Denno 2005; Berger et al. 2008). Thus, IGP and IK have become a popular topic among ecologists, wildlife managers, and conservation biologists.

Intraguild predation and interspecific killing are both associated with some well-defined behavioral attributes (Arim and Marquet 2004). In communities of carnivorous mammals, the largest and behaviorally most dominant species influence the population sizes, behaviors, and distribution of subordinate

species through both predation and competitive displacement (e.g., Lindstrom et al. 1995; Mills and Gorman 1997; Creel et al. 2001; Kamler et al. 2003). Thus, IGP and IK are often highly asymmetric in carnivores (Palomares and Caro 1999; Linnell and Strand 2000), where both frequency and intensity of killing and/or predation reach a maximum when the larger species is 2–5.4 times the mass of the victim (Donadio and Buskirk 2006). Patterns of predator species grouping behavior also appear to play an important role; social carnivores kill larger species than solitary ones (Palomares and Caro 1999). Predatory habits and predator taxonomic relatedness are also influential in predisposing carnivores to attack each other. Species that routinely eat vertebrate prey are more prone to interspecific killing; in addition, carnivorans tend to interact more with species in the same taxonomic family than with species in different families (Donadio and Buskirk 2006).

Palomares and Caro (1999) first quantified the distribution of interspecific killing among mammalian carnivorans, analyzing 97 different pairwise interactions involving 54 victim and 27 killer species. They showed that mortality from carnivores killing a victim through IGP or IK interactions was 38 % (ranging from 4 to 76 %). Further specific contributions on carnivores have proliferated (e.g., Sunde et al. 1999; Fedriani et al. 2000; Berger and Gese 2007), and IGP and IK have been demonstrated to be fundamental determinants of the structure of carnivoran assemblages. For this reason, IGP and IK have become important considerations in conservation management, since threatened species may face possible negative impacts from other carnivores that are capable of killing them (Laurenson 1995; Creel and Creel 1996; Durant 1998; Linnell and Strand 2000; Podra et al. 2013).

Caro and Stoner (2003) and Hunter and Caro (2008) assessed the potential for interspecific competition and predation within the assemblages of mammalian carnivorous species in Africa and the Americas. Their continental-scale approaches captured the diversity of potential killing interactions within large sets of carnivorans (70 species in Africa and 77 in the Americas), including species with different degrees of phylogenetic relatedness and variation in range overlap. However, these authors did not validate their findings with specific records of predation events. Thus, empirical data on the frequency and distribution of IGP and IK interactions within these assemblages are still lacking.

Forty native terrestrial carnivoran species occur in South America, including eleven canids, one bear, eight procyonids, seven mustelids, three skunks, and ten felids. These species share many common attributes that may predispose them to competitive interactions (Hunter and Caro 2008). For example, several of these species are known to coexist throughout vast geographic areas, showing considerable overlap in range and habitat usage (e.g., jaguar *Panthera onca*, puma *Puma concolor*, bush dog *Speothos venaticus*, tayra *Eira barbara*, and South American coati *Nasua nasua*). Most South American carnivoran species are generalists (e.g., canids, procyonids), but hypercarnivores (felids) are also widespread. Although the range in body size may span up to two orders of magnitude (average body mass = 1.2 kg for olingos *Bassaricyon* spp. and 120 kg for the spectacled bear *Tremarctos ornatus*), small-bodied (<7 kg) carnivorans predominate, with more than 70 % of all these species classified in this category. In spite of all these factors indicating a high potential for competition, only one attempt has been made to investigate the role of IGP/IK in structuring carnivoran community assemblages in South America (see Oliveira et al. 2010; Oliveira 2011 for a case with felids).

The goal of the current study was to assess the extent and potential role of intraguild predation and interspecific killing as significant forces influencing carnivoran assemblages in South America. To accomplish this, we gathered all of the available data on diet and predation for South American terrestrial carnivoran species, and estimated the number of potential intraguild predators for each.

Methods

We included all 40 species of terrestrial Carnivora found in South America in our analysis. However, all olingo species (*Bassaricyon alleni*, *Bassaricyon beddardi*, *Bassaricyon gabbii*), and all South American weasels (*Mustela africana*, *Mustela felipei*, *Mustela frenata*) were grouped as *Bassaricyon* spp. and *Mustela* spp. due to their high degree of ecological similarity and general paucity of data on individual species. Data on white-nosed coatis *Nasua narica* were combined with that for South American coatis, because the former has a very limited distribution in South America and is ecologically and morphologically equivalent to the latter.

To assess the extent of IGP and IK within the terrestrial South American carnivoran assemblage we obtained records from published and unpublished sources (papers, thesis, reports, field observations, and unpublished data of carnivoran specialists). To investigate the potential of IGP and IK to have a significant ecological influence, we compared the mean mass of all species whose ranges did not overlap marginally (established at >20 %). As competitive interactions should be the principle cause of IK events, the species diets and extent of overlap in habitat use were also compared. Body mass data, obtained from Redford and Eisenberg (1992), Eisenberg and Redford (1999), Sillero et al. (2004), and Oliveira and Cassaro (2005), were averaged across genders and populations for each species. The extent of geographic range overlap for each pair of species was determined by overlaying range maps taken from Oliveira (1994), Eisenberg and Redford (1999), Sillero et al. (2004), Oliveira and Cassaro (2005), and the IUCN database (IUCN 2013).

To assess dietary overlap among species, the feeding habits of all species were classified according to 11 different categories: fruits/plant material, insects, crustaceans, other invertebrates, fish, amphibians/reptiles, birds, small mammals (<1 kg), medium sized mammals (1–15 kg), large mammals (> 15 kg), and carrion. Each food category was ranked as main (+++), moderate (++), occasional (+), or absent (0) item, according to its relative frequency of occurrence in each species diet. Aspects of the sociality (i.e., solitary, pairs, groups), activity (i.e., diurnal, crepuscular, nocturnal), and habitat use (we used broad categories such as Tropical rainforest, Subtropical rainforest, Tropical deciduous/semideciduous forest, Tropical thorny forest and scrubland, Semi-arid thorny scrub, Savanna, Wet/swampy savanna, Premontane forest, Montane forest, Temperate forest / Southern rainforest, Monte desert / Semi-desert, Patagonian steppes / scrub, High altitude semi-arid steppes and scrub, and Open grassland) of each carnivoran species were also considered. Diet, sociality, and habitat data were taken from Eisenberg and Redford (1999), Oliveira (2002, unpubl. data), Sillero et al. (2004), Wilson and Mittermeier (2009), and Oliveira et al. (2010). Nomenclature follows Wozencraft (2005), except for the Pampas cat *Leopardus colocolo* group, which we considered to represent a single species.

Potential intraguild predator species were identified as those having overlapping ranges and body masses 2–5.4 times larger than other guild members (Donadio and Buskirk 2006). Additionally, we categorized likely-potential intraguild predator species as those that were also either hypercarnivorous or, at least, those for which vertebrates are a considerable part of their diets. Donadio and Buskirk (2006) observed that at the above mentioned size range the frequency and intensity of carnivoran interspecific killing reaches a maximum, as there is higher potential for considerable dietary overlap and, consequently, higher benefit for the larger species to eliminate the smaller potential competitors. For this reason, only species with carnivorous diet were considered to be likely-potential predators. Predominantly omnivorous South American Carnivora would hardly interact in such a way.

Statistical analyses included testing for normality prior to using parametric or non-parametric tests. Tests included correlation analysis of body mass for killers and victims, paired comparisons of the number of potential and likely-potential intraguild predators, and comparisons of the number of events where a particular species was the killer or the victim.

Results and Discussion

Diet, behavior, and habitat use data all suggested that the potential for interespecific competition was high in South American carnivoran assemblages (Tables S1, S2, and S3). As such, there would be a potential benefit for the dominant potential competitor to eliminate subordinate species. The potential number of intraguild predators for the 35 species evaluated here ranged from zero to 18, with an average of 5.35±SE 0.74, and a median of four (Table 1). Of all these species, only nine could not be considered potential intraguild predators. This is due to a combination of their limited geographic ranges, small body sizes, and low degree of carnivory in their diets. Thus, 26 species (74.3 %) of the assemblage could be considered potential intraguild predators. Only jaguars and spectacled bears were judged to not have any potential predators, whereas lesser grisons *Galictis cuja* (18), weasels (16), olingos (12), Molina's hog-nosed skunks *Conepatus humboldtii* and mountain coatis *Nasuella olivacea* (11 each), and oncillas *Leopardus tigrinus* (10) showed the greatest number of potential killers. Considering only adults, 94 % of the assemblage could be under threat from intraguild predation. However, when the analysis was limited to only the most likely potential predator species (i.e., species with mostly a carnivorous diet), the number declined to only 14 species (40 %). Thus, likely potential killers per species ranged from 0 to 12, with an average of 3.5±SE 0.45 and a median of three (Table 1). Paired comparisons for the number of potential and likely potential intraguild predator species showed significant differences (W =-264.000, T+= 6.000, T-=-270.000, P <0.001). Both results (potential and likely potential killers) were similar to those found for intraguild predation in Africa (Caro and Stoner 2003). A review of 599 potential intraguild predators and 763 potential intraguild prey found intraguild predation to be common in nature, with frequencies ranging from 58.4 to 86.7 % (Arim and Marquet 2004). These previously reported values were well within the values estimated here, except those for likely potential killers, for which our results were notably smaller.

We obtained 116 records of IGP/IK events for terrestrial Neotropical carnivoran species in South America. These interactions involved 52 pairs of species. Thirteen species involved in these interactions were identified as killers and 25 as victims (Tables 2 and 3). There was a significant difference between the number of interactions where a species was the killer or the victim (T =522.5, P =0.002, n =26). Thus, confirmed intraguild predators accounted for 37.1 % of all carnivoran species, about the same as those predicted to be likely potential predators (n =13 and 14, respectively). Considering the mean ratios, each killer species has, on average, 5.60 times±SE 1.74 (1.2–20.9, n =13) the mean mass of their victims. However, when taking the mean of all species pairs, these values rise to 12.01±SE 3.14 (1–156.8, n =52). This was undoubtedly a consequence of the higher ratios shown by species pairs involving jaguars and pumas, the species with the highest number of recorded killing events. The higher the ratio, the lower the potential gain from IK, because niche overlap is expected to decrease among species as their body sizes differences increase (Woodward and

Table 1 Potential for intraguild predation (IGP) and interspecific killing (IK) within South American terrestrial Carnivora

Species	Common name	Weight (kg)	Minimum predator mass required for IGP or IK (kg)[a]	Number of potential predators	Likely predator
Lycalopex culpaeus	Culpeo	7.3	14.6	1	Puma
Lycalopex fulvipes	Darwin's fox	2.7	5.4	2	Puma, culpeo
Lycalopex griseus	Chilla fox	3.2	6.4	2	Puma, culpeo
Lycalopex gymnocercus	Pampas fox	5.0	10	3	Puma, jaguar(?)
Lycalopex sechurae	Sechura fox	3.6	7.2	2	Puma, culpeo
Lycalopex vetulus	Hoary fox	3.4	6.8	5	Maned wolf, ocelot, puma, jaguar
Atelocinus microtis	Short-eared dog	7.8	15.6	2	Jaguar, puma
Cerdocyon thous	Crab-eating fox	5.7	11.4	4	Maned wolf, ocelot, puma, jaguar
Speothos venaticus	Bush dog	6	12	3	Jaguar, puma, ocelot?
Chrysocyon brachyurus	Maned wolf	25	50	1	Puma, jaguar
Urocyon cinereoargenteus	Gray fox	3.7	7.4	5	Jaguar, puma, ocelot
Tremarctus ornatus	Spectacled bear	105	210	0	0
Procyon cancrivorus	Crab-eating racoon	8.8	17.6	3	Jaguar, puma
Nasua nasua/Nasua narica	Coati	3.9	7.8	6	Ocelot, jaguar, puma
Nasuella olivacea	Mountain coati	1.2	2.4	11	Culpeo, spectacled bear, ocelot, margay, oncilla, Pampas cat, jaguarundi, puma, jaguar
Potos flavus	Kinkajou	2.4	4.8	9	Ocelot, jaguarundi, puma, jaguar
Bassaricyon spp.	Olingos	1.2	2.4	12	Ocelot, margay, jaguarundi, puma, jaguar
Mustela spp.	Weasels	0.25	0.5	16	Ocelot, margay, oncilla, jaguarundi, puma, jaguar, gray fox?
Galictis vittata	Greater grison	2.7	5.4	8	Bush dog, ocelot, puma, jaguar
Galictis cuja	Lesser grison	1.6	3.2	18	Culpeo, chilla fox, bush dog, maned wolf, ocelot, margay, Andean cat, Geoffroy's cat, Pampas cat, jaguarundi, puma, jaguar
Lyncodon patagonicus	Patagonian weasel	0.25	0.5	8	Culpeo, chilla fox, Andean cat, Geoffroy's cat, Pampas cat, puma
Eira barbara	Tayra	4.6	9.2	4	Ocelot, puma, jaguar
Conepatus semistriatus	Striped hog-nosed skunk	2.4	4.8	9	Bush dog, maned wolf, ocelot, puma, jaguar
Conepatus chinga	Molina's hog-nosed skunk	1.8	3.7	11	Culpeo, chilla fox, Pampas fox, ocelot, Geoffroy's cat, Pampas cat, jaguarundi, puma, jaguar
Conepatus humboldtii	Humboldt's hog-nosed skunk	1.3	2.6	6	Culpeo, chilla fox, Geoffroy's cat, Pampas cat, Andean cat, puma
Leopardus pardalis	Ocelot	11	22	3	Puma, jaguar
Leopardus wiedii	Margay	3.3	6.6	6	Ocelot, puma, jaguar
Leopardus tigrinus	Oncilla	2.4	4.8	10	Ocelot, puma, jaguar
Leopardus guigna	Guiña	1.7	3.4	3	Culpeo, puma
Leopardus jacobitus	Andean cat	4	8	2	Puma
Leopardus geoffroyi	Geoffroy's cat	4.3	8.6	4	Ocelot, puma, jaguar
Leopardus colocolo	Pampas cat	3.5	7	5	Ocelot, puma, jaguar
Puma yagouaroundi	Jaguarundi	5.2	10.4	4	Ocelot, puma, jaguar
Puma concolor	Puma	39.2	78.4	1	Jaguar
Panthera onca	Jaguar	61.4	122.8	0	0

[a] Following Donadio and Buskirk (2006), we considered each focal species at risk of being killed by other carnivorans if body mass of predator species is at least two times larger than the focal species' body mass

Hildrew 2002). Thus, there should be a body size limit to the ecological gain from eliminating potential competitors.

There was a strong, significant, and positive correlation between body mass of killers and mean mass of victims ($r=0.950$,

Table 2 Records of intraguild predation and interspecific killing within terrestrial South American carnivorans

Killer	Victim	Number of areas reported	Source
Panthera onca	*Cerdocyon thous*	1	A. Paviolo pers. comm.
	Nasua spp.	11	Rabinowitz and Nottingham 1986; Crawshaw 1995; Aranda and Sanchez-Cordero 1996; Garla et al. 2001; Hass and Valenzuela 2002; Nuñez et al. 2002; Perovic 2002; Azevedo 2008; Palacio 2010; A. Paviolo pers. comm.
	Procyon cancrivorus	5	Garla et al. 2001; Polisar et al. 2003; Scognamillo et al. 2003; Azevedo 2008; Palacio 2010
	Potos flavus	3	Rabinowitz and Nottingham 1986; Chinchilla 1997; Garla et al. 2001
	Bassaricyon sp.	1	Emmons 1987
	Eira barbara	2	Crawshaw 1995; A. Paviolo pers. comm.
	Leopardus pardalis	3	Chinchilla 1997; González-Maya et al. 2010; R. Leite-Pitman unpubl. data
	Leopardus wiedii	2	Crawshaw 1995; Perovic 2002
	Leopardus sp.	2	Taber et al. 1997; Garla et al. 2001
	Puma concolor	2	Crawshaw and Quigley 1984; P. Perovic unpubl. data
Puma concolor	*Cerdocyon thous*	2	Brito 2000; A. Paviolo pers. comm.
	Lycalopex gymnocercus	2	Pessino et al. 2001; Wander unpubl. data
	Lycalopex culpaeus	4	Iriarte et al. 1991; Novaro et al. 2005; Pacheco et al. 2004; Elbroch and Wittmer 2013
	Lycalopex griseus	4	Yañez et al. 1986; Johnson and Franklin 1994; Skewes et al. 2012; A. Valenzuela pers. comm.
	Lycalopex vetulus	1	E. Lima pers. comm.
	Chrysocyon brachyurus	1	J.P. Santos pers. comm.
	Urocyon cinereoargenteus	1	Monroy-Vilchis et al. 2009
	Nasua spp.	9	Crawshaw 1995; Aranda and Sanchez-Cordero 1996; Brito 2000; Hass and Valenzuela 2002; Nuñez et al. 2002; Moreno et al. 2006; Martins et al. 2008; Monroy-Vilchis et al. 2009; Palacio 2010; A. Paviolo pers. comm.
	Nasuella olivacea	1	Hernández-Guzmán et al. 2011
	Procyon cancrivorus	1	Brito 2000
	Potos flavus	1	Brito 2000
	Galictis cuja	4	Pessino et al. 2001; Zapata 2005; Palacio 2010; Zanon-Martínez et al. 2012
	Mustela sp.	1	Monroy-Vilchis et al. 2009
	?Eira barbara	1	Farrell et al. 2000
	Conepatus semistriatus	1	Wolff 2001
	Conepatus chinga	4	Pessino et al. 2001; Pacheco et al. 2004; Zanon-Martínez 2006; Skewes et al. 2012
	Conepatus humboldtii	3	Iriarte et al. 1991; Johnson and Franklin 1994; G. Aprile pers. comm.
	Leopardus sp.	1	Branch et al. 1996
	Leopardus geoffroyi	2	Zanon-Martínez 2006; Pereira et al. 2010
	Leopardus colocolo	1	Zanon-Martínez 2006
	Puma yagouaroundi	2	Crawshaw 1995; Martins et al. 2008
Leopardus pardalis	*Cerdocyon thous*	1	Crawshaw 1995
	Nasua spp.	4	Gompper and Decker 1998; Moreno et al. 2006; Palacio 2010; Rocha-Mendes et al. 2010
	Procyon cancrivorus	3	Crawshaw 1995; Moreno et al. 2006; Bianchi et al. 2010
	Potos flavus	1	Bianchi et al. 2010
	Bassaricyon sp.	1	Emmons 1987
	Eira barbara	1	Bianchi et al. 2010
	Galictis cuja	1	Crawshaw 1995

Table 2 (continued)

Killer	Victim	Number of areas reported	Source
	Leopardus wiedii	1	T.G. de Oliveira pers. obs.
	Leopardus tigrinus	1	T.G. de Oliveira pers. obs.
Leopardus wiedii	*Nasua nasua*	1	Wang 2002
	Galictis cuja	2	Wang 2002; Rinaldi 2010
Leopardus tigrinus	*Nasua nasua*	1	Rocha-Mendes et al. 2010
Leopardus colocolo	*Galictis cuja*	1	Zapata et al. 2007
Leopardus geoffroyi	*Conepatus chinga*	1	J. Pereira pers. obs.
Puma yagouaroundi	*Nasua nasua*	1	Gompper and Decker 1998
	Lycalopex gymnocercus	1	P. Perovic pers. comm.
Chrysocyon brachyurus	*Lycalopex vetulus*	3	Jácomo et al. 2004; J. Dalponte unpubl. data
	Cerdocyon thous	1	Rodrigues et al. 2007
	Canidae	1	Rodrigues et al. 2007
	Galictis cuja	2	Juarez and Marinho-Filho 2002; Jácomo et al. 2004
Lycalopex culpaeus	*Galictis cuja*	1	Zapata et al. 2005
	Conepatus humboldtii	2	Johnson and Franklin 1994; Zapata et al. 2005
Lycalopex griseus	*Galictis cuja*	1	Zapata et al. 2005
	Conepatus humboldtii	2	Johnson and Franklin 1994; Zapata et al. 2005
Lycalopex gymnocercus	*Conepatus chinga*	1	Castillo et al. 2011
Galictis cuja	*Conepatus humboldtii*	1	Zapata et al. 2005

$P=0.0000007$, $N=13$). This suggests that size is indeed quite relevant to IGP and IK behavior. Palomares and Caro (1999) found a similar trend, with weight of victim increasing with weight of solitary killers. We did not focus on the actual consumption of victims, but based on the diet studies we assessed (references on Table 2), it seemed to be a widespread outcome. However, there were also instances where this did not happen.

Some interesting patterns also emerged from our data. Jaguars, pumas, and ocelots were identified as killers in

Table 3 Family summary of intraguild predation and interspecific killing within the South American terrestrial carnivoran assemblage

Family	Number of killer species (% all species in the family/ all species)	Number of species killed (% all species in the family/ all species)	Number of interactions where one species was the killer	Number of interactions where one species was killed
Canidae	4 (36.4)	7 (63.6)	14	23
Procyonidae	–	5 (100)	–	44
Ursidae	–	–	–	–
Mustelidae	1 (20)	3 (60)	1	17
Mephitidae	–	3 (100)	–	15
Felidae	8 (80)	7 (70)	101	17
Total	13 (37.1)	25 (71.4)	116	116

80 % of the cases that were considered here. These three felid species are also the largest bodied hypercarnivores in South America. In this way, IGP/IK events are highly concentrated among hypercarnivorous species, whereas ca. 51 % of the victim species were the omnivorous procyonids and skunks (Table 3). These results support the hypothesis of Hunter and Caro (2008) regarding the high potential IGP pressure faced by skunks, but contradicts the low potential IGP pressure predicted for procyonids. Although these authors conjectured that procyonids may reduce intraguild predation pressure by altering their spatial and temporal use of resources, our data were conclusive with respect to their high frequency as intraguild prey items. It is also likely that procyonids were highly represented as victims due to their overall abundance, which is the highest for all Neotropical carnivoran species (Robinson and Redford 1989).

Most of the records presented here consist of IGP feeding events and not competitive exclusion through IK. That is to say, 51.1 % of all killer-victim pairs should represent IGP feeding events, and thus, were not related to interference competition. Nevertheless, species with a predominantly carnivorous diet killing another meat eating species, which defines the essence of IK, i.e., the killing of a potential competitor, accounted for just 26.1 % of all killing events involving South American carnivorans. Of all pairs of predator mass-victim mass ratios, 45.3 % were up to 5.4 times the body mass of the victim species, which could indicate that there is

significant benefit from competitive exclusion (Donadio and Buskirk 2006). Of the three main intraguild predators, 77.8 % of all ocelot victim species fell within the range reported by Donadio and Buskirk (2006) indicating some competitive gain, whereas jaguars and pumas represented only 22.2 % and 16.7 %, respectively. This finding suggests that the medium-sized ocelot may be the most impacting species of the South American terrestrial carnivoran guild with respect to IGP and IK pressures. It has been previously shown that ocelots have a negative impact on smaller sized, sympatric species, an observation known as the "ocelot effect" (Oliveira et al. 2010; Oliveira 2011). The findings presented here could further expand the potential influence of this felid species on other members of the guild, beyond other felids. The ocelot's medium size makes it more prone to overlap with other felids and thus confers to it some advantage from interspecific killing by way of competitive release, compared to the much larger big cats.

Maned wolves *Chrysocyon brachyurus*, Pampas foxes *Lycalopex gymnocercus* and, to a lesser extent, chilla foxes *Lycalopex griseus*, were the only killer species whose diet was not mostly carnivorous, i.e., about 77–85 % of known intraguild predators are hypercarnivores. The omnivorous coatis were the most frequently killed carnivorans and also the only species that actually showed some importance as a component of killer species diets (found in about 35 % of jaguar diet studies). However, for both jaguars and pumas, carnivoran species accounted for just a minor portion of their diet (<5 %, 0–22.1 %, see review by Oliveira 2002). Despite this, IGP on hypercarnivores could also be very representative. Both in Costa Rica and Amazonian Peru, jaguar predation on ocelots was found to be high (Gonzalez-Maya et al. 2010; R. Leite-Pitman unpubl. data). Although they show considerable body size differences, their diets have several items in common (Oliveira et al. 2010) and their mass ratio of 5.4 is indeed within the range suggested for species having the highest potential gain from IK. The second most preyed upon species was the small (1.6 kg) and highly carnivorous lesser grison.

Some of the cases reported here were not expected, given the mass of the species involved. An adult oncilla (2.4 kg, 1.8–3.5 kg, Oliveira and Cassaro 2005) or margay *Leopardus wiedii* (3.3 kg, 2.3–4.9 kg, Oliveira and Cassaro 2005) would unlikely kill an adult coati, which weighs considerably more than the cats (3.9 kg, 2–7.2 kg, Eisenberg and Redford 1999), besides presenting fierce behavior (Hass and Valenzuela 2002). As such, events like these (and probably the one involving lesser grison predation on a Humboldt's hog-nosed skunk) likely represent predation upon young/juvenile individuals (ca. 40 % of adult mass, or 1.56 kg, value that we considered for the ratio calculation between these felids and the coati). Palomares and Caro (1999) noted that some interacting species are only able to kill non-adults of the other

species, which was probably the case for these particular events. If predation upon non-adults is taken into account, then the number of potential intraguild predators rises considerably for most species.

For the Andean region and the southern cone, besides pumas, only culpeo foxes *Lycalopex culpaeus* and, to a lesser extent chilla foxes, Geoffroy's cat *Leopardus geoffroyi*, Pampas cats, and Andean cats *Leopardus jacobita* could act as intraguild predators. In the tropical regions of South America, besides pumas and Pampas cats, killer species also include jaguars, ocelots, jaguarundis *Puma yagouaroundi*, margays, oncillas, maned wolves, and bush dogs. Evidence of interactions among these carnivoran species (e.g., Scrocchi and Halloy 1986; Oliveira 2011; Lucherini and Luengos Vidal 2003; P. Perovic pers. comm.; T. Oliveira pers. obs.) suggests that, although exploitative and/or interference competition may be operating, IGP and IK would be unlikely between species whose body mass ratios are <2. Additionally, the current rarity and distribution of some species (e.g., bush dogs, Oliveira 2009; and Patagonian weasels *Lyncodon patagonicus*, Schiaffini et al. 2013) could be a product of competitive interactions with larger carnivorans. These interactions warrant further investigation and pose some interesting hypotheses to be tested.

Concluding Remarks

Our results showed that jaguars, pumas, and ocelots were the most likely species to have an impact on the structure of the Neotropical carnivoran guild. Of these three species, it is likely that the medium-sized ocelots exert the greatest impact, as this species attains higher densities and would also benefit more from competitive release than the much larger cat species. Although our results may be potentially biased, due to the higher volume of data available for felids compared to other taxonomic groups (e.g., mustelids), the observed pattern is indicative of a strong role played by these felids as intraguild predators.

Most interactions within the South American carnivoran assemblage seemed to be more related to dietary purposes (IGP) than of a competitive nature (IK). Nevertheless, both IGP and IK could potentially be affecting the structure of communities and at least be partially responsible for shaping the evolutionary history of some species. Our findings are consistent with the idea that intraguild predation and interspecific killing are not random and represent widespread interactions that should be involved in structuring carnivoran communities in South America.

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