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COMPARATIVE FEEDING ECOLOGY OF JAGUAR AND PUMA IN THE NEOTROPICS

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Abstract

Jaguar (*Panthera onca*) and puma (*Puma concolor*) have similar body sizes and share many of the same range and habitats. In order to better understand their ecological differentiation, their macroecological patterns of trophic utilization and dietary segregation were assessed. Dietary breadth of both species were very similar. Prey utilization was extremely variable, but consisted predominantly of peccaries, deer, large caviomorph rodents, and armadillos. Differences in their consumed biomass in sympatry were found only for peccaries and chelonians. Jaguars consumed more medium and larger sized mammals (> 1 kg), whereas puma ate more medium sized mammals (1–15 kg). Nevertheless, no differences were found between these predators for any of the prey weight-class sizes. Their patterns of prey selection were probably influenced by prey availability and vulnerability. Food overlap ranged from 17% to 82%, but even in areas of high overlap

there were differences in the proportions of some prey taken. Jaguar and puma mean prey weight (MPW) varied considerably but, on average, that of jaguar was twice as much as the puma's. A similar trend was noted for the mean mass of main prey. However, if only MPW of wildlife were considered, no differences were found. MPW differed by habitat type for both cats. For both predator species, larger prey were taken in the floodplains (puma also on xeric areas of the USA/Mexican border) and the smallest in drier South American habitats. MPW was positively correlated with jaguar ($r = 0.660$) and puma ($r = 0.833$) body size. The mean prey-predator ratio (MPPR) was similar for both felids, whereas jaguar:puma body and MPW ratios showed the same patterns in Central (1:0.9) and South America (1:0.6). Trends found were indicative of dietary segregation, possibly to minimize competition.

Resumo

A onça-pintada (Panthera onca) e a suçuarana (Puma concolor) apresentam tamanho corporal, distribuição geográfica e habitats semelhantes. Para uma melhor compreensão das suas diferenciações ecológicas, seus padrões macroecológicos de utilização trófica e segregação alimentar foram avaliados. A amplitude do nicho alimentar de ambas espécies foi muito semelhante. A utilização de espécies-presa foi extremamente variável, mas consistiu predominantemente de porcos-do-mato, veados, grandes roedores caviomorfos e tatus. Diferenças na biomassa consumida em simpatria foram encontradas somente para porcos-do-mato e quelônios. A onça-pintada consumiu mais mamíferos de médio-grande porte (> 1 kg), enquanto a suçuarana consumiu predominantemente mamíferos de médio porte (1–15 kg). Entretanto, nenhuma diferença foi encontrada entre estes predadores para qualquer das classes de tamanho das presas. Os padrões de seleção das presas foram provavelmente influenciados pela disponibilidade e vulnerabilidade destas. A sobreposição alimentar variou entre 17% e 82%, mas mesmo em áreas de alta sobreposição houveram diferenças nas proporções de algumas espécies-presas. O peso médio das presas (PMP) da onça-pintada e da suçuarana variou consideravelmente mas, em média, o da onça-pintada foi duas vezes maior que o da suçuarana. Um padrão similar também foi observado para a biomassa média das presas principais. Por outro lado, quando somente o PMP das presas silvestres foi considerado, nenhuma diferença foi encontrada. O PMP variou também entre

os tipos de habitat para ambas espécies. Tanto a onça-pintada quanto a suçuarana pegaram presas de maior porte nas planícies alagadas (a suçuarana também nas áreas secas da fronteira EUA/México) e as menores nos habitats secos da América do Sul. O PMP apresentou correlação positiva com o tamanho corporal tanto da onça-pintada ($r = 0.660$) quanto da suçuarana ($r = 0.833$). A razão média presa:predador foi similar para ambos predadores, enquanto a razão onça-pintada:suçuarana para tamanho corporal e PMP apresentaram os mesmos padrões na América Central (1:0.9) e América do Sul (1:0.6). As tendências encontradas foram sugestivas de uma segregação alimentar, possivelmente para minimizar competição.

1. Introduction

The jaguar (*Panthera onca*) and the puma (*Puma concolor*) are the largest felids in the Neotropical region. Throughout most of their range they live sympatrically and, as they have some overlap in size and occupy many of the same habitats, they should present some level of ecological segregation.

Terborgh (1990, 1992) has suggested that the abundance of prey species in the Neotropics, and consequently, their effect on the plant community, could be directly influenced by the predatory patterns of jaguar and puma. Therefore, these large carnivores could ultimately influence the entire community. Additionally, predators could also affect their prey indirectly. The prey could alter their behavior, could use different habitats and food sources and/or reduce their foraging time, thus minimizing the risk of being preyed upon (Schmitz, 1998). Understanding the intricate prey selection patterns and the ecological segregation of large carnivores provides very important information for the conservation and management of these “keystone/umbrella species” and, ultimately, for community conservation (Karanth and Sunquist, 1995; Miller and Rabinowitz, this volume; Miller et al., in review; Nuñez et al., in review).

Several studies of jaguar and puma food habits have showed a large degree of prey utilization and dietary adaptability (e.g., Crawshaw, 1995; Emmons, 1987; Iriarte et al., 1990; Oliveira, 1994a; Rabinowitz and Nottingham, 1986; Taber et al., 1997). Although their trophic differentiation have been reviewed by Jorgenson and Redford (1993) and Oliveira (1994a), the number of studies in sympatry at the time were small (three), as well as were most of the sample sizes (McBride, 1976 - only six stomach contents for jaguars; Emmons, 1987 - seven scats for puma) with the exception of Crawshaw and Quigley (this volume). In the light of new and larger datasets on jaguar and puma diet, both sympatrically and not, I assess in this paper the macroecological patterns of trophic utilization and, especially, the interactions between these large felids in the Neotropical region.

2. Methods

Information on food habits of jaguars and pumas were obtained from 23 studies, eight of which from areas of sympatric occurrence. Prey were divided into three groups,

based on their mean adult mass, small (<1 kg), medium (1–15 kg), and large (> 15 kg). To determine the biomass consumed by felids, the geometric grand mean of all vertebrate prey weight (MPW) was estimated (Jaksic 1983). Additionally, MPW of the main prey for each area was also estimated. Main prey were those taxa that comprised the bulk (usually >70% when combined) of jaguar and puma items taken in each study site. All prey were assumed to be adults, unless noted otherwise. Prey mass, whenever possible, was obtained from the original studies, otherwise they came from the literature, especially Redford and Eisenberg (1992). For cattle, I used 80 kg for calf class size (< 2-years-old), and 175 kg for adults (> 2-years-old), hence the differences from other previous studies. For a more accurate estimation of prey selectivity patterns, I calculated the relative biomass consumed (data from scats only) using Ackerman et al.'s (1984) correction factor:

$$Y = 1.98 + 0.035X$$

where Y is the mass of food consumed per scat and X is the live mass of prey. This would compensate the overrepresentation of small prey and the underestimation of larger animals (Ackerman et al., 1984; Karanth and Sunquist, 1995; Nuñez et al., in review). Additionally, I compared the distribution of prey by weight-class size of the relative biomass consumed with those of the biomass taken (i.e., average MWVP of each class size).

Levins' (1968) food niche breadth was calculated at the lowest taxonomic level possible (i.e., species):

$$B = 1/\sum p_i^2$$

where p_i is the relative proportion of prey taxon i in the diet. It ranges from one to the number of prey categories. In order to allow comparisons among studies with different prey categories the standardized food-niche breadth (B_{sta} ; Colwell and Futuyma, 1971) was estimated:

$$B_{sta} = (B_{obs} - B_{min}) / (B_{max} - B_{min})$$

where B_{obs} is the observed breadth of the diet, B_{min} is the minimum breadth of diet (= 1), and B_{max} is the maximum breadth possible (i.e., the number of prey taxa taken). Trophic niche overlap was calculated according to Pianka's index (1973), which ranges between 0 (no overlap) and 1 (complete overlap).

Data in the form of percentages were converted into arcsin ($y_t = \arcsin \sqrt{y}$) for statistical analyses (Ott, 1988). Statistics included one-way ANOVA, paired t-test, chi-square, and analysis of correlation. Significance level was considered at $P < 0.05$.

3. Results and Discussion

• Dietary Breadth

The standardized food-niche breadth (B_{sta}) of both jaguar and puma varied, but were, on average, very similar (0.43 for jaguar, and 0.45 for puma; Tabs. 1, 2; $F = 0.10$, $P = 0.759$). Considering only studies in sympatry and with large sample sizes ($N > 30$; Tab. 3), the results would remain the same, as in some areas jaguars took a wider prey base (Crawshaw, 1995; Crawshaw and Quigley, this volume; Taber et al., 1997), whereas on others puma diet was more variable (Brito et al., 1998; Garla, 1998; Nuñez et al., in review). This B_{sta} similarity was the opposite of the common belief that jaguars have a more restricted diet than pumas (e.g., Jorgenson and Redford, 1993; Nuñez et al., in review; Oliveira, 1994a). In fact, both cats are opportunistic hunters taking whatever is available.

Differences in the B_{sta} values presented herein and those reported by Iriarte et al. (1990), Jorgenson and Redford (1993), and Oliveira (1994a) were due to its estimation at class/group level by those authors, whereas here it was calculated at the lowest taxonomic level possible (i.e., species level).

• Mean Prey Weight

The mean prey weight (MPW) consumed by jaguar (31 ± 31.84 kg) and puma (13.85 ± 14.04 kg) varied considerably among all study sites (Tabs. 1, 2). That of jaguar was, on average, more than twice that of puma ($F = 4.58$, $P = 0.041$). However, if only sympatric areas were considered ($N = 8$; Tab. 3), no differences were found (mean = 21.1 ± 27.21 kg for jaguar, 14.80 ± 16.46 kg for puma; $F = 0.36$, $P = 0.560$). The average mass of jaguar main prey (41.1 ± 36.9 kg) was also larger than that of the puma (16.6 ± 16.5 kg; $F = 5.29$, $P = 0.029$), but not in sympatric areas ($F = 0.33$, $P = 0.573$). Pairwise comparisons of main prey and the average MPW differed significantly for both jaguar ($t = 3.980$, $df = 16$, $P = 0.001$) and puma ($t = -2.596$, $df = 13$, $P = 0.022$).

Mean prey mass of jaguar ranged from 2.39 kg in the Chaco to 62.9 kg in the northern Pantanal of Brazil (mean from scat analysis). The southern-Pantanal estimate of 87.7 kg (the highest) was not directly comparable because it was based on kill analysis, not on feces (Crawshaw and Quigley, this volume). Analysis of kill data tend to overestimate the importance of larger, more detectable prey, whereas smaller prey are virtually not detected. In the northern Pantanal, MPW based from kills was 73.9 kg (Schaller, 1983 and Dalponte, this volume, combined), whereas from scats it was 62.9 kg (Dalponte, this volume). Clearly, the use of kill data leads to an overestimation of the mean prey weight. Similar results have been found by Karanth and Sunquist (1995) for tiger, leopard and dhole in India. Puma MPW ranged from 1.48 kg in the Paraguayan Chaco to 29.1 kg in Torres del Paine National Park, southern Chile. Again, as already mentioned, the southern Pantanal value (52.3 kg) was not directly comparable (Crawshaw and Quigley, this volume). Considering MPW of wildlife only, jaguar's mean (14.42 ± 8.63 kg) was similar to that of the puma (12.06 ± 9.68 kg; $F = 1.14$, $P = 0.295$), even if only sympatric areas were considered ($F = 0.40$, $P = 0.537$). The differences between these cats overall MPW and $MPW_{wildlife}$ were a consequence of jaguar inclusive predation on adult cattle and puma being more restricted to calves, whereas the natural prey base was the same.

Strong positive correlations between felid body mass and their mean prey mass have already been reported by Iriarte et al. (1990) for puma (including North American populations) and Oliveira (1994a) for the jaguar. Using a much larger dataset for both jaguar (17 study areas, as opposed to eight) and puma (14 areas, instead of seven), I reevaluated the correlations and found similar results to those studies before, both for jaguar ($r = 0.660$, $P = 0.004$) and puma ($r = 0.833$, $P < 0.001$; Neotropical populations only).

The mean prey-predator ratio (MPPR) of jaguar (0.46 ± 0.39) was larger than the puma's (0.31 ± 0.25), as a consequence of predation on livestock, but not significantly different ($F = 1.54$, $P = 0.224$). If livestock were excluded from the analysis their MPPR were almost identical (0.22 ± 0.11 for jaguar; 0.22 ± 0.15 for puma - does not include kill data for both species). MPPR for main prey showed the same trend, with jaguar's average (0.58 ± 0.50) larger than the puma's (0.37 ± 0.29), but not significantly different ($F = 1.93$,

$P = 0.176$). In areas of sympatry, their main prey MPPR were identical (mean = 0.37; $F = 0$, $P = 1.00$).

Jaguar/puma mean prey weight ratio in sympatry was 1.66 ± 0.70 (Tab. 3), meaning that the average jaguar prey was about 39% (18–65%) larger than that of the puma, with the exception of Campeche (Mexico), where the puma average prey was 54% larger than the jaguar's. Looking at continental level, jaguar:puma body ratio was more equal in Central (1:0.9) than South America (1:0.6). Interestingly, the mean prey weight ratio of these felids also carried the same proportions in Central (1:0.9) and South America (1:0.6). This suggests that where they are more equal sized, their average prey mass are more similar, as previously noted by Nuñez et al. (in review). Although the number of studies for comparisons are still small ($N = 8$), these ratios equality seems to confirm Sunquist and Sunquist (1989) suggestion that the size of large predators are constrained by the size of available prey.

In comparison to other large felids, including North American puma, the mean prey weight of jaguar and Neotropical puma was smaller (e.g., Bailey, 1993; Iriarte et al., 1990; Karanth and Sunquist, 1995; Kruuk and Turner, 1967; Schaller, 1972;) as well as their MPPR (Karanth and Sunquist, 1995; Packer, 1986). This is likely a consequence of unavailability of very large wild prey in the Neotropics. The largest wild prey available in the region are tapir (Tapirus terrestris, 177 kg; and Tapirus bairdii, 275 kg) and marsh deer (Blastocerus dichotomus, 109 kg) in tropical areas, and guanaco (Lama guanicoe, 120 kg) in temperate areas (Redford and Eisenberg, 1992). Large ungulates are not representative of Neotropical faunal assemblages, as opposed to their exuberance in Africa and Asia. This leads to lower biomass in forested areas in the Neotropics (1,416 kg/km² in Manu-Peru, 3,361 kg/km² on BCI-Panama; Jason and Emmons, 1990; Glanz, 1990, respectively) compared to some forests in Asia where the biomass can reach 17,870 kg/km² (Karanth and Sunquist, 1992). Biomass estimates are even lower when one considers open habitats in the Neotropics (380 kg/km², 3,750 kg/km² including cattle in the Brazilian Pantanal, 946 kg/km² and 1,086 kg/km² in the Llanos of Venezuela; Schaller, 1983; Eisenberg et al., 1979, respectively) compared to some savannas in Africa, where the biomass can reach 8,713 kg/km² (Bailey, 1993). This invariably leads to the higher mean prey weight of the

large cats of the old world (e.g., Bailey, 1993; Karanth and Sunquist, 1995; Kruuk and Turner, 1967; Schaller, 1972).

- Diet Composition

Prey utilization by jaguar and puma was extremely variable among areas (Tabs. 1, 2), supporting evidence for a generalist predation pattern, emphasizing locally abundant prey. Mammals comprised the bulk of both number of prey and biomass consumed by jaguar and puma (Figs. 1, 2). However, in areas where reptiles, notably chelonians, were abundant, they became important components of jaguar diet, but not of the puma (Carrillo and Saenz, this volume; Emmons, 1987, 1989). Jaguar ability to use chelonians as prey items, a resource not used by puma, is likely related to its more robust and powerful jaws (Van Valkenburgh and Ruff, 1987). Birds were only occasionally taken and did not contribute significantly to the biomass consumed. Thus, they were not considered overall important components of the diets of jaguar and puma.

Peccaries, large caviomorph rodents (especially capybaras), deer, armadillos, reptiles, and small carnivores (especially coatis) comprised the bulk of jaguar diet (Tab. 1). Relative biomass consumed of these main prey differed ($F = 2.53$, $P = 0.027$). Peccaries were consumed more than all other species ($P < 0.05$), except deer, from which the difference was only marginally insignificant ($P = 0.054$). Thus, they seemed to be the preferred food item (they were found in the diet in every study area, mostly as major prey). Selective predation by jaguar upon peccaries has been noted in several studies along the cats entire range (Aranda, 1994; Carrillo and Saenz, this volume; Crawshaw 1995; Emmons, 1987).

The main components in the diet of the puma were similar to that of the jaguar, consisting of deer, large caviomorph rodents (especially paca), armadillos, peccaries, and lagomorphs (especially in temperate areas; Tab. 2). In North America, on the other hand, puma predation was predominantly upon deer (Iriarte et al., 1990) and, contrary to that of the jaguar, the relative biomass of main prey consumed (tropical areas) by puma did not differ ($F = 1.78$, $P = 0.141$). Significant differences were found only when all prey consumed were compared ($F = 3.12$, $P = 0.002$).

Of their main prey, jaguars took, on average, more peccaries and large reptiles (especially chelonians and caimans) than puma, which preyed more on deer, opossums, large and small rodents than jaguar. Nevertheless, between-site variation in the consumption of these prey-species by both predators was high, precluding significance (except for caimans; $F = 4.47$, $P = 0.048$). Meanwhile, differences between biomass consumed by jaguar and puma in sympatric areas were found for peccaries ($F = 8.40$, $P = 0.013$) and chelonians ($F = 5.14$, $P = 0.043$), but not for any other prey species ($P > 0.05$).

Cattle was also an important prey for both predators. However, puma depredation was almost exclusive on calves, whereas the jaguar also included adult animals (Boulhosa and Valdes, 1997; Crawshaw and Quigley, this volume; González-Fernández, this volume; Hoogesteijn et al., 1993; Perovic, this volume). Puma predation on livestock also includes a great deal of sheep and goats (P. Crawshaw, pers. com.; McBride, 1976; Yañez et al., 1986).

The prey base used by both felids throughout their range was largely the same (Tabs. 1, 2). However, the proportions of different prey species taken by jaguar and puma varied among sites. This resulted in a low food-niche overlap in some areas and medium-high in others (Tab. 3). Even in the latter situation, there were still significant differences in the proportions of some prey used. This was the case for the forests of Jalisco-Mexico ($\chi^2 = 33.63$, $P < 0.001$; Nuñez et al., in review) and Espírito Santo-Brazil ($\chi^2 = 101.81$, $P < 0.001$; Brito et al., 1998 and Garla, 1998, combined), for the floodplains of the Brazilian Pantanal ($\chi^2 = 28.97$, $P = 0.004$; Crawshaw and Quigley, this volume), and for the dry Paraguayan Chaco ($\chi^2 = 14.99$, $P < 0.05$; Taber et al., 1997). Notwithstanding, in the subtropical forest of Iguazu-Brazil there was no difference in prey utilization between jaguar and puma ($\chi^2 = 24.33$, $P = 0.060$). In this area, biomass of peccaries and deer accounted for 93% of the biomass taken by jaguars and 82% by puma (Crawshaw, 1995). Apparently, segregation in this area must be taking place in some other way.

High levels of food-niche overlap have been found for several carnivore species (e.g., Major and Sherburne, 1987; Ray, 1996; Waser, 1980), including small Neotropical felids (Oliveira and Paula, in review), showing that high overlaps are not uncommon among carnivores. As Pimm (1991) pointed out, there could be extensive overlap among predators in the exploitation of common, abundant prey, and that segregation would occur

through selection of different, rarer, less common prey. This seems to be the case between jaguar and puma.

- Predation by weight-class size

Jaguars consumed significantly more medium and large animals than smaller ones (Tab. 4; $F = 34.95$, $P < 0.001$). However, consumption of medium and larger prey was virtually identical ($F = 0.01$, $P = 0.918$). Conversely, puma consumption was different among every weight-class size (Tab. 5; $F = 22.89$, $P < 0.001$), even between medium and large prey ($F = 9.57$, $P = 0.006$). For this species, medium-sized mammals comprised the bulk of the relative biomass consumed. Meanwhile, no differences were found between jaguar and puma for any of the class sizes of the relative biomass consumed ($< 1\text{kg}$: $F = 1.18$, $P = 0.290$; $1\text{--}15\text{ kg}$: $F = 2.11$, $P = 0.162$; $> 15\text{ kg}$: $F = 2.53$, $P = 0.127$). The trends for the biomass of animals taken were exactly the same as those for consumption ($P > 0.05$). This lack of significant difference may be a consequence of their similarities in body size (see comments under Mean Prey Weight). The only difference that could be noted as far as prey weight-class sizes of these two cats are concerned, is that only in Torres del Paine (southernmost Chile) did puma prey on very large wild prey ($> 50\text{ kg}$) in the Neotropics, an area where jaguars do not exist (Iriarte et al., 1990, 1991; Yañez et al., 1986). The jaguar, on the other hand, did so throughout most of its range: in Amazonian rainforests (Kuroiwa and Ascorra, this volume; Oliveira, pers. obs.), Atlantic rainforests (Garla, 1998), premontane Yungas forests (Perovic, this volume), Pantanal floodplains (Almeida, n.d.; Crawshaw and Quigley, this volume; Dalponte, this volume; Schaller, 1983), savannas (L. Silveira, pers. com.), and Chaco (Taber et al., 1997). This would differentiate them in areas of common range distribution.

There were highly significant differences in the mean values between the proportions of the biomass taken and the relative biomass consumed indices for class sizes $> 1\text{ kg}$ for jaguar (Tab. 4; $1\text{--}15\text{ kg}$, $P = 0.009$; $> 15\text{ kg}$, $P = 0.005$), but none were found for puma (Tab. 5; $P = 0.290$, $P = 0.162$, $P = 0.127$). Given the difference found, and as the corrected estimates are the least biased (Ackerman et al., 1984; Karanth and Sunquist, 1995), studies dealing with food habits should incorporate these parameters in their analysis for a more accurate assessment of predator-prey relations.

- Predation by habitat type

There were significant differences in mean prey weight by habitat type for both jaguar ($F = 7.80$, $P = 0.006$; Tab. 6) and puma ($F = 5.08$, $P = 0.013$; Tab. 7). For puma calculations, I included data from the Everglades floodplain in Florida, and grouped northern Mexico estimates with those from adjacent Arizona and New Mexico (from Iriarte et al., 1990). On the other hand, no differences in diet breadth were found among habitats for either jaguar ($F = 1.09$, $P = 0.365$) or puma ($F = 1.15$, $P = 0.382$). Differences in mean prey weight among several habitat types have also been found for leopards (Oliveira, 1994b). Considering all main prey species's biomass consumed among vegetation types, no differences were found for jaguars ($P > 0.05$). No such comparison could be performed for puma, due to data limitations.

Overall, larger prey were taken by jaguars in the floodplains, and the smallest in xeric areas (not considering data from northern Mexico, which included livestock and animals from another zoogeographical faunal assemblage). Forest prey species were intermediate in size (no differences were found between moist and dry forests, and between Central and South American forests, $P > 0.05$). For pumas, larger prey were taken in the floodplains and xeric areas of the US/Mexican border region and the smallest in drier areas of South America. It is possible that prey availability and vulnerability are higher in floodplains than in forested regions (Hoogesteijn and Mondolfi, 1996) and drier South American habitats. Additionally, in Neotropical floodplains, both felids relied greatly on livestock (Crawshaw and Quigley, this volume; Dalponte, this volume; Hoogesteijn and Mondolfi, 1996), which substantially increased their mean prey weight. Nevertheless, even if only wild prey is considered, that taken by jaguar in floodplains (mean = 26.9 kg) would still significantly outrank that of forests (mean = 11.72 kg; $F = 13.18$, $P = 0.003$) in the ratio of 2:1. This proportion differed from that previously reported (ca. 6:1), which was likely due to its much smaller sample size. If livestock were included, ratios would be ca. 5:1 (this study) versus 15:1 (Hoogesteijn and Mondolfi, 1996).

Hoogesteijn and Mondolfi (1996) found that site effect on jaguar body mass were highly significant. Since cat mass was positively correlated with mean prey mass,

differences in mean prey weight among major habitat types were to be expected. No such correlations have been made for puma, but the same pattern seems to take place.

Despite differences in food utilization, jaguar and puma also have shown some level of spatial segregation, with the latter avoiding the first (Crawshaw and Quigley, 1984; Schaller and Crawshaw, 1980), except for Jalisco-Mexico (Nuñez et al., this volume). However, in this dry forest of Mexico, there was food segregation (Nuñez et al., in review). Oliveira (1994a) suggested dominance of jaguars on puma, based on evidence from field studies, paleontological record, and by comparing other predators elsewhere. This apparent dominance would likely result from the larger jaguar body mass, i.e., be a consequence of character displacement. The findings in Jalisco further support this, as body mass of both felids there were on the same range, with some pumas being even larger than some jaguars (Nuñez et al., this volume).

The trends found in this analysis were indicative of dietary segregation between jaguars and pumas, as well as of a generalist predation pattern centered on locally abundant prey by both predators. Additionally, this in depth comparative look of the macroecological patterns of trophic utilization and interactions between Americas' largest felids should be an important tool for the management and conservation of these "umbrella species" in this new millennium.

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Table 1. Distribution of jaguar prey by size and taxonomic group (percentage of occurrence).

PREY ITEMS	Tamau lipas Mex. ¹	Jalisco Mex. ²	Cam- peche Mex. ³	Belize ⁴	Costa Rica ⁵	Vene- zuela ⁶	Manu Peru ⁷	Tambo -pata Peru ⁸	NE - Brazil ⁹	Panta- nal Braz. ¹⁰	N-Pant Braz. ¹¹ (scat)	N-Pant Braz. ¹² (kill)	S-Pant Braz. ¹³	Esp. Santo Braz. ¹⁴	Iguaçu Braz. ¹⁵	Para- guay ¹⁶	NW- Arg. ¹⁷
LARGE PREY (>15 kg)	83.3	57.2	50	11.1	31.9	72.2	20.5	14.4	14.3	59.3	30.7	58.6	84.7	30.8	47	31.9	44.4
Deer	16.7	41.3	8	5.2	4.5	–	5.1	–	–	–	3.8	11.4	1.7	2.9	9	23.5	7.2
Peccaries	33.3	15.9	42	5.9	18.3	11.1	15.4	14.4	14.3	18.6	3.8	5.7	30.5	27.2	38	4.6	8.9
Other large mamm.	–	–	–	–	–	5.6	–	–	–	3.7	–	–	5.1	0.7	–	3	2.9
Livestock	33.3	–	–	–	–	55.5	–	–	–	37	23.1	41.4	47.4	–	–	–	25.4
Rheas / Turtles	–	–	–	–	9.1	–	–	–	–	–	–	–	–	–	–	0.8	–
MEDIUM PREY (1–15 kg)	16.7	33.3	42	75.5	68.1	27.8	56.4	28.8	71.4	40.7	65.5	41.4	15.3	65.5	50	22.1	23.3
Opossums	–	1.6	–	3	–	–	2.6	–	–	–	–	–	–	–	10	5.3	0.8
Armadillos	–	14.3	12	44.4	4.5	–	–	4.8	14.3	–	–	–	–	22.1	9	7.6	0.8
Other Edentates	–	–	2	7	18.3	–	2.6	4.8	57.1	3.7	–	1.4	1.7	2.1	–	1.5	4.7
Monkeys	–	–	–	–	9	–	2.6	4.8	–	–	–	–	–	1.4	1	–	–
Carnivores	16.7	17.4	18	2.2	4.5	–	2.6	–	–	7.4	11.6	–	–	22.1	8	0.8	2.1
Large Rodents	–	–	4	14.8	4.5	–	15.3	14.4	–	22.2	40.5	31.4	13.6	8.5	6	6.1	12.2
Large Birds	–	–	6	–	4.5	5.6	–	–	–	–	3.8	–	–	0.7	9	–	1.3
Chelonians	–	–	–	2.2	–	–	23.1	–	–	–	–	–	–	7.9	–	0.8	–
Caimans	–	–	–	–	–	11.1	7.6	–	–	7.4	9.6	8.6	–	–	–	–	–
Large Lizards/snakes	–	–	–	1.9	22.8	11.1	–	–	–	–	–	–	–	0.7	7	0.8	1.3
SMALL PREY (<1 kg)	–	9.5	–	9.2	–	–	10.3	56.4	–	–	–	–	–	–	3	42.4	26.3
Small Marsupials	–	–	–	0.7	–	–	2.6	9.6	–	–	–	–	–	–	–	5.3	–
Small Rodents	–	–	–	5.2	–	–	2.6	22.9	–	–	–	–	–	–	2	13.6	16.1
Rabbits	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	6.4
Small Birds	–	3.2	–	–	–	–	–	23.9	–	–	–	–	–	–	–	–	0.4
Small Reptiles	–	6.3	–	2.6	–	–	–	–	–	–	–	–	–	–	–	–	–
Other taxa	–	–	–	0.7	–	–	5.1	–	–	–	–	–	–	–	–	–	3.4
Unknown (mamm., birds, reptiles)	–	–	8	4.2	–	–	12.2	–	14.3	–	3.8	–	–	3.5	–	3.1	5.9

Table 1. Cont.

Sample Size ^a	6 S	50 F	37 F	302 F	22 F	18 S	25 F	13 F	7 F	26 S	35 F	70 K	59 K	101 F	73 F	106 F	
MPW (kg)	73.5	15.6	13.5	6.8	12.4	50	10.7	5.2	6.2	52.4	62.9	73.9	87.7	11.7	14.8	2.4	44.7
Main prey MPW (kg)	97.0	17.5	14.7	8.0	14.0	80	13.4	7.3	7.6	64.6	89.1	86.3	97.3	11.3	18.6	8.6	62.8
Mean cat mass (kg)	49.2	49.2	49.2	49.2	49.2	85.7	35	35	50	87.6	87.6	87.6	87.6	80	80	50	80
MPPR	1.50	0.32	0.27	0.14	0.25	0.58	0.31	0.15	0.12	0.60	0.72	0.99	1.00	0.15	0.18	0.05	0.56
Diet Breadth	3.60	3.97	4.21	4.40	7.10	2.85	11.17	3.55	2.58	4.90	3.80	3.47	3.33	11.6	5.28	7.38	8.76
B _{sta}	0.87	0.50	0.36	0.18	0.61	0.37	0.60	0.23	0.53	0.49	0.47	0.35	0.29	0.48	0.30	0.29	0.37

^a F = scats; S = stomach contents; K = kill

1- McBride (1976); 2- Nuñez et al. (In review); 3- Aranda & Sánchez (1996); 4- Rabinowitz & Nottingham (1986) and Watt (1987) combined; 5- Chinchilla (1997); 6- Hoogesteijn & Mondolfi (1993); 7- Emmons (1987); 8- Kuroiwa & Ascorra (this volume); 9- Olmos (1993); 10- Almeida (unp.); 11- Dalponte (this volume); 12- Schaller (1983) and Dalponte (this volume) combined; 13- Crawshaw & Quigley (this volume); 14- Garla (1998); 15- Crawshaw (1995); 16- Taber et al. (1997); 17- Perovic (this volume).

Table 2. Distribution of puma prey by size and taxonomic group (percentage of occurrence).

PREY ITEMS	N-Mex. ¹	Jalisco Mex. ²	Campeche Mex. ³	Costa Rica ⁴	Manu Peru ⁵	Río Abiseo Peru ⁶	S-Pantanal Brazil ⁷	Esp. Santo Brazil ⁸	Iguaçu Brazil ⁹	Paraguay ¹⁰	C-Argentina ¹¹	C-Chile ¹²	S-Chile ¹³	Southern-most Chile ¹⁴
LARGE PREY (>15 kg)	86	44.3	60	8.3	–	–	67.8	17.9	29.7	24.4	22.5	9.5	3.6	27.7
Deer	48.8	37.1	50	8.3	–	–	13	17	13.5	11.8	–	–	–	0.5
Peccaries	4.6	7.2	10	–	–	–	–	–	16.2	9	–	–	–	–
Camelids	–	–	–	–	–	–	–	–	–	–	1.6	–	–	17.1
Other large mamm.	–	–	–	–	–	–	–	–	–	2.7	–	–	–	–
Livestock	32.6	–	–	–	–	–	51.6	0.9	–	–	20.9	9.5	3.6	10.1
Rheas	–	–	–	–	–	–	3.2	–	–	0.9	–	–	–	–
MEDIUM PREY (1–15 kg)	14	15.4	40	66.6	58.3	33.3	32.2	79.1	64.9	25.3	62.8	90.5	74.7	68
Opossums	–	1	5	8.3	–	–	–	0.9	16.2	8.2	–	–	–	–
Armadillos	–	9.3	5	–	–	–	3.2	13.2	27.1	10.8	4.8	–	–	–
Other Edentates	–	–	–	–	–	–	–	0.9	–	1.8	–	–	–	–
Monkeys	–	–	–	33.3	–	–	–	5.7	–	–	–	–	–	–
Carnivores	–	4.1	20	–	–	–	–	19.8	5.4	–	1.6	–	–	6.6
Small deer	–	–	–	–	–	–	–	–	–	–	–	81	26.8	–
Large Rodents	14	–	5	8.3	58.3	33.3	29	35.8	5.4	4.5	51.6	–	–	–
Hares	–	–	–	–	–	–	–	–	–	–	4.8	–	45.8	54
Large Birds	–	–	5	–	–	–	–	–	–	–	–	9.5	2.4	7.4
Large Reptiles	–	1	–	16.7	–	–	–	2.8	10.8	–	–	–	–	–
SMALL PREY (<1 kg)	–	40.3	–	–	16.7	66.7	–	0.9	5.4	43.7	14.6	–	–	3.9
Small Marsupials	–	3.1	–	–	–	–	–	–	–	8.2	–	–	–	–
Small Rodents	–	18.6	–	25	16.7	66.7	–	0.9	5.4	26.4	14.6	–	–	3.9
Rabbits	–	–	–	–	–	–	–	–	–	9.1	–	–	–	–
Small Birds	–	2.1	–	–	–	–	–	–	–	–	–	–	–	–
Small Reptiles	–	16.5	–	–	–	–	–	–	–	–	–	–	–	–
Other taxa	–	–	–	–	8.3	–	–	–	–	–	–	–	–	–
Unknown (mamm., birds, reptiles)	–	–	–	–	16.7	–	–	–	–	6.4	–	–	–	0.4

Table 2. Cont.

Sample Size ^a	54 S	65 F	15 F	11 F	7 F	9 F	31 K	74 F	28 F	95 F	44 F	21 K	65 F	747 F
MPW (kg)	25.2	12.7	20.6	5.4	3.7	2.0	52.3	8.3	10.8	1.5	4.8	12.7	4.9	29.1
Main prey MPW (kg)	34.8	14.8	25.9	3.2	6.2	5.0	61.0	8.9	12.4	5.73	4.5	9	5.5	32.7
Mean cat mass (kg)	43.6	43.6	43.6	43.6	28	28	56.5	40	40	35.4	35	32.2	32.2	55.6
MPPR	0.58	0.29	0.47	0.12	0.13	0.07	0.93	0.21	0.27	0.04	0.14	0.39	0.15	0.52
Diet Breadth	3.05	4.85	3.23	6.55	4.24	5.55	3.58	6.31	5.28	11.2	3.20	1.50	3.25	2.90
B _{sta}	0.41	0.38	0.37	0.79	0.29	0.65	0.43	0.33	0.30	0.68	0.24	0.24	0.28	0.34

^a F = scats; S = stomach contents; K = kills

1- McBride (1976); 2- Nuñez et al. (In review); 3- Aranda & Sánchez (1996); 4- Chinchilla (1997); 5- Emmons (1987); 6- Romo (1995); 7- Crawshaw & Quigley (this volume); 8- Brito et al. (1998); 9- Crawshaw (1995); 10- Taber et al. (1997); 11- Branch et al. (1996); 12- Courtin et al. (1980); 13- Rau et al. (1991); 14- Iriarte et al. (1990).

Table 3. Comparative parameters of the diets of jaguar and puma in areas of sympatric occurrence (Sources: see Tabs. 1, 2).

Site	B _{sta}		MPW (kg)		Main prey MPW (kg)		Jaguar/ Puma MPW ratio	Dietary Overla p
	Jaguar	Puma	Jaguar	Puma	Jaguar	Puma		
Jalisco - Mexico	0.50	0.38	15.60	12.74	17.50	14.84	1.22	0.84
Campeche - Mex.	0.35	0.37	13.49	20.64	14.69	25.86	0.65	0.31
Costa Rica	0.61	0.79	12.44	5.10	13.95	2.81	2.44	0.39
Manu - Peru	0.60	0.29	10.70	3.71	13.40	6.24	2.88	0.26
Esp.Santo - Brazil	0.48	0.33	11.74	8.31	11.30	8.90	1.41	0.49
Iguaçu - Brazil	0.30	0.72	14.78	10.80	18.59	12.39	1.37	0.72
Paraguay	0.29	0.68	2.39	1.48	8.64	5.73	1.61	0.78
S-Pantanal - Brazil (kill)	0.29	0.43	87.70	52.30	97.19	61.05	1.68	0.82
Overall mean	0.43	0.50	21.10	14.80	24.41	17.23	1.66	0.58
	± 0.14	± 0.20	± 27.21	± 16.46	± 29.58	± 19.10	± 0.70	± 0.24
Scat mean	0.45	0.51	11.59	8.97	14.01	10.97	1.65	0.54
	± 0.14	± 0.21	± 4.4	± 6.49	± 3.42	± 7.74	± 0.76	± 0.24

Table 4. Distribution of jaguar prey (number, biomass taken, relative biomass consumed¹) by weight-class size (numbers in percentage; sources: see Tab. 1).

Site	Number			Biomass taken			Relat. biomass consumed ¹		
	< 1 kg	1–15 kg	> 15 kg	< 1 kg	1–15 kg	> 15 kg	< 1 kg	1–15 kg	> 15 kg
Tamaulipas-Mx	–	16.7	83.3	–	2.9	97.1	–	–	–
Jalisco-Mx	9.5	33.3	57.2	0.3	10.4	89.3	2.1	28.5	69.4
Campeche-Mx	–	45.7	54.3	–	17.2	82.8	–	40.2	59.8
Belize	6.4	81.6	12.0	0.3	53.8	46.1	1.0	82.3	16.7
Costa Rica	–	77.3	22.7	–	32.9	67.1	–	70.1	29.9
Venezuela	–	27.8	72.2	–	3.2	96.8	–	–	–
Manu-Peru	6.3	65.6	28.1	0.3	38.4	61.3	1.5	62.3	36.2
Tambopata-Peru	57.1	28.6	14.3	4.5	27.0	68.5	7.2	56.0	36.8
NE-Brazil	–	83.3	16.7	–	55.2	44.8	–	80.4	19.6
Pantanal-Br	–	22.2	77.8	–	2.8	97.2	–	–	–
N-Pantanal-Br (scat)	–	26.0	74.0	–	2.8	97.2	–	13.8	86.2
N-Pantanal-Br (kill)	–	10.0	90.0	–	2.4	97.6	–	–	–
S-Pantanal-Br	–	1.6	98.4	–	0.08	99.92	–	–	–
Esp. Santo-Br	–	71.2	28.8	–	29.4	70.6	–	67.4	32.6
Iguaçu-Br	12.0	41.0	47.0	0.6	8.5	90.9	1.0	38.9	60.1
Paraguay	45.5	22.7	31.8	2.9	4.5	92.6	17.0	22.5	60.5
NW-Argentina	25.2	23.0	51.8	0.1	1.8	98.1	0.6	7.6	91.8

¹ Scats samples only

Table 5. Distribution of puma prey (number, biomass taken, relative biomass consumed¹) by weight-class size (numbers in percentage; sources: see Tab. 2).

Site	Number			Biomass taken			Relat. biomass consumed ¹		
	< 1 kg	1–15 kg	> 15 kg	< 1 kg	1–15 kg	> 15 kg	< 1 kg	1–15 kg	> 15 kg
N-Mexico	–	14.0	86.0	–	1.9	98.1			
Jalisco-Mx	39.1	14.2	46.7	1.1	5.7	93.2	0.1	24.6	75.3
Campeche-Mx	–	40.0	60.0	–	8.9	91.1	–	30.4	69.6
Costa Rica	25.0	66.7	8.3	1.8	55.6	42.6	0.1	85.5	14.4
Manu-Peru	27.3	63.7	–	1.4	98.6	–	3.5	96.5	–
Río Abiseo-Peru	60.0	40.0	–	2.1	97.9	–	4.7	95.3	–
S-Pantanal-Br	–	3.2	96.8	–	0.2	99.8			
Esp. Santo-Br	1.0	78.8	20.2	0.03	52.4	47.6	0.1	76.9	23.0
Iguaçu-Br	5.4	64.9	29.7	0.03	18.4	81.6	0.1	60.8	39.1
Paraguay	50.0	25.0	25.0	2.2	7.1	90.7	13.0	34.0	53.0
C-Argentina	14.9	61.2	23.9	0.5	52.3	48.1			
C-Chile	–	90.5	9.5	–	65.2	34.8			
S-Chile	21.7	74.7	3.6	0.2	81.2	18.6	0.6	93.4	6.0
Southernmost-Chile	3.9	68.4	27.7	0.03	8.3	91.7	0.03	47.3	52.6

¹ Scats samples only

Table 6. Jaguar predation by habitat type.

Habitat type	B_{sta}	Mean Prey Weight	N
Forested areas	0.39 ± 0.16	15.1 ± 11.6	9
Floodplains	0.41 ± 0.09	69.3 ± 29.6	4
Xeric areas	0.56 ± 0.29	27.4 ± 40.0	3

Table 7. Puma predation by habitat type.

Habitat type	B_{sta}	Mean Prey Weight	N
Tropical forests	0.48 ± 0.22	10.2 ± 6.1	6
Floodplains	0.40 ± 0.04	34.7 ± 24.9	2
Temperate areas	0.38 ± 0.19	12.2 ± 12.1	4
Southern xeric areas	0.60 ± 0.12	3.1 ± 2.4	2
Northern xeric areas	0.25 ± 0.23	35.3 ± 8.8	3

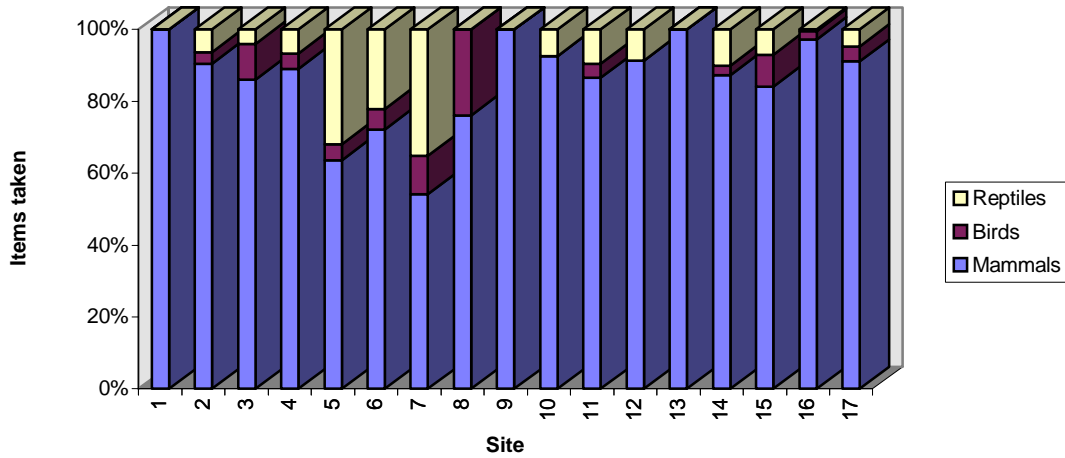


Figure 1. Number of jaguar prey items by class (1- Tamaulipas/Mx, 2- JaliscoMx, 3- Campeche/Mx, 4- Belize, 5- Costa Rica, 6- Venezuela, 7- Manu/Peru, 8- Tambopata/Peru, 9- NE-Brazil, 10- Pantanal/Br, 11- N-Pantanal/Br (scat), 12- N-Pantanal/Br (kill), 13- S-Pantanal/Br, 14- Espírito Santo/Br, 15- Iguazu/Br, 16- Paraguay, 17- NW-Argentina).

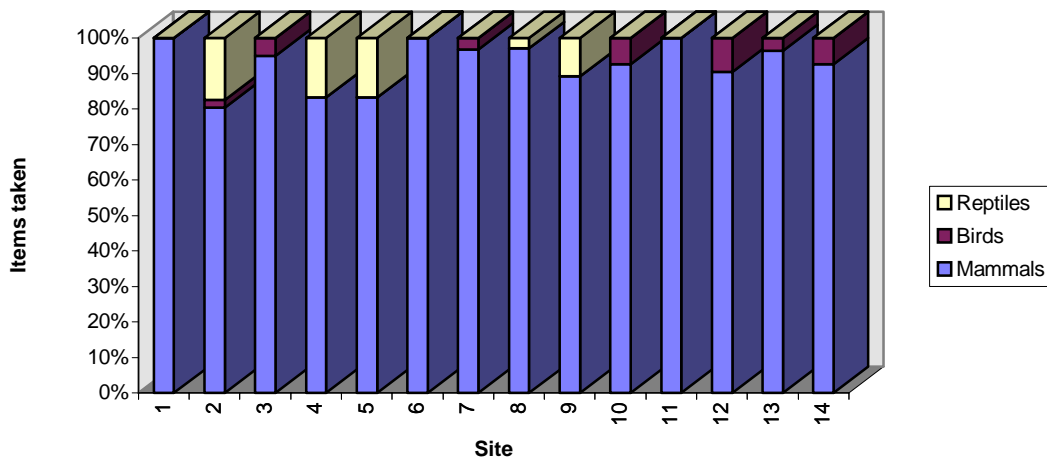


Figure 2. Number of puma prey items by class (1- N-Mexico, 2- Jalisco/Mx, 3- Campeche/Mx, 4- Costa Rica, 5- Manu/Peru, 6- Río Abiseo/Peru, 7- S-Pantanal/Br, 8- Espírito Santo/Br, 9- Iguazu/Br, 10- Paraguay, 11- C-Argentina, 12- C-Chile, 13- S-Chile, 14- Southernmost-Chile).