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A morphological comparison of jaguars and pumas in southern Mexico

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Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are sympatric throughout the entire range of the jaguar. Pumas are smaller in areas where they are sympatric with jaguars and their body size is larger outside the distribution range of jaguars. This pattern has been explained as an effect that natural selection has promoted through character displacement to partially avoid competition. We examined and compared the body and craniodental measurements of sympatric jaguars and pumas from a tropical rainforest in southern Mexico. Data on body sizes were obtained from jaguars and pumas captured with foot snares. We implemented a principal component analysis (PCA) to evaluate variability in sizes between species and sexes and to characterize groups of individuals according to these morphological variables. Finally, we compared morphological variables using analyses of variance (ANOVAs) and pairwise comparisons using the Bonferroni adjustment. Body size and mass of female jaguars were similar to male pumas in southern Mexico. But, canines and mouth breadth were larger in female jaguars than in male pumas. In general, male jaguars were larger than male pumas and female jaguars were larger than female pumas, throughout the distribution of the jaguar. However, female jaguars and male pumas may have similar body mass and size in much of their sympatric distribution. Our results suggest that character displacement between jaguars and pumas might be expressed not only by their body size, but also by their skull size, the length and robustness of canines, and the mouth breadth, and these morphological differences allow for resource partitioning and the coexistence of these two species that have very similar ecological requirements.

Jaguares (*Panthera onca*) y pumas (*Puma concolor*) son simpátricos a lo largo de toda la distribución del jaguar. Los pumas son de menor tamaño en las áreas de simpatría con el jaguar y su tamaño incrementa en las áreas en donde los jaguares no están presentes. Este patrón se ha explicado como un resultado de la selección natural promovido a través del desplazamiento de caracteres para evitar la competencia, al menos parcialmente. En este estudio, examinamos y comparamos las medidas del cuerpo y cránio-dentales de jaguares y pumas de un bosque lluvioso tropical del sur de México. La información del tamaño corporal fue obtenida de jaguares y pumas capturados con trampas de lazo en el sureste de México. Se realizó un análisis de componentes principales para medir la variabilidad en el tamaño entre especies y sexos y para caracterizar grupos de individuos de acuerdo a estas variables morfológicas. Finalmente, se compararon las variables morfológicas usando un análisis de varianza y pruebas de comparación de pares utilizando el ajuste de Bonferroni. Nuestros resultados indican que el tamaño del cuerpo y el peso son similares entre las hembras de jaguar y los pumas machos. Sin embargo, el largo y robustez de los caninos y la amplitud de la boca son más grandes en las hembras de jaguar que en los pumas machos. En general, los machos de jaguar son más grandes que los pumas machos y las hembras de jaguar son más grandes que las hembras de puma a lo largo de la distribución del jaguar. Sin embargo, las hembras de jaguar pueden tener masa y tamaño corporal similar al de los pumas machos en gran parte de su distribución simpátrica. Nuestros resultados sugieren que el desplazamiento de caracteres entre pumas y jaguares podría expresarse no solamente en el tamaño corporal, sino también por la longitud y robustez de los colmillos y la amplitud de la boca. Estas diferencias morfológicas probablemente han permitido la repartición de recursos y la coexistencia de estas dos especies que tienen requerimientos ecológicos muy similares.

Keywords: Body size; canines; Mexico; *Panthera onca*; *Puma concolor*.

Introduction

The jaguar (*Panthera onca*) and the puma (*Puma concolor*) are the largest felids in the Neotropics since the Late Pleistocene, and these species constitute the guild of large apex predators in terrestrial ecosystems there. Jaguars and pumas are sympatric throughout the entire range of the jaguar, and pumas are smaller in areas where they are sympatric with the jaguar, but they have a larger body size outside the areas of jaguar distribution (Iriarte *et al.* 1990; Sunquist and Sunquist 2009). This pattern has been explained as a type of character displacement facilitating avoidance of competition (Iriarte *et al.* 1990). Character displacement is defined as the process in which differences in one or more morphological characters among similar species with overlapping distributions are accentuated as a result of inter-specific competition in regions where the species occur together; these differences are minimized or lost where the distributions of the two species do not overlap (Brown and Wilson 1956; Dayan *et al.* 1990; Jones 1997; Pfennig and Pfennig 2009).

Although jaguars are larger than pumas where they are sympatric, there is overlap in their size and the size of prey they can hunt effectively; for this reason, several authors have considered them as potentially competing species (Taber *et al.* 1997; Nuñez *et al.* 2000; Scognamillo *et al.* 2003; Novack *et al.* 2005; Azevedo 2008; Rosas-Rosas *et al.* 2008; Foster *et al.* 2010). Several studies have examined the interactions between these species in areas of sympatry.

It appears that coexistence between jaguars and pumas is facilitated by using different habitats (Scognamillo *et al.* 2003), active avoidance of the same sites (Harmsen *et al.* 2009; Sollmann *et al.* 2012; de la Torre *et al.* 2017), temporal segregation (Romero-Muñoz *et al.* 2010), or by differential use of prey (Emmons 1987; Jorgeson and Redford 1993; Aranda and Sánchez-Cordero 1996; Taber *et al.* 1997; Nuñez *et al.* 2000; Scognamillo *et al.* 2003; Novack *et al.* 2005). However, few studies have analyzed the differences in body sizes and other morphological characters of these coexisting species (Kiltie 1984; Morales and Giannini 2010), especially from data obtained directly from animals of the same study area.

We examined and compared body and cranio-dental measures of sympatric jaguars and pumas in a tropical rainforest of Mexico. Because pumas are smaller in areas where they are sympatric with the jaguar (Iriarte *et al.* 1990), we predicted that morphological characteristics of these species would differ in southern Mexico. Given that felid species are strongly sexually dimorphic and each sex of a guild of felids can be considered as morphologically distinct (Dayan *et al.* 1990; Jones 1997), we also predicted that morphological characteristics would differ within each species between males and females.

Materials and methods

Data on body sizes of jaguars and pumas were obtained from the Greater Lacandona Ecosystem (GLE) in southeastern Mexico (Medellín 1994; de la Torre and Medellín 2011). Jaguars and pumas were captured in foot snares and fitted with GPS radio-collars (Frank *et al.* 2003; de la Torre *et al.* 2017). At the site of each snare trap, we also placed a VHF radio transmitter to monitor if traps were triggered (Halstead *et al.* 1995). Traps were checked every four hours throughout the night and, depending on weather conditions, several times during the day to respond immediately to any capture. All capture and handling protocols followed the IACUC Guidelines of the American Society of Mammalogists (Sikes *et al.* 2011). Permission to conduct the field captures was granted by the General Office of Wildlife-SEMARNAT (2010-No.11347). After capture, we immobilized jaguars using a dose of 0.08 mg/kg of medetomidine combined with 5 mg/kg of ketamine, and pumas using a dose 0.08 mg/kg of medetomidine combined with 6 mg/kg of ketamine. Immobilization dosage was administrated using a dart fired from a CO_2 pistol or rifle. While the animal was immobilized, we examined individual body condition and determined sex. We estimated age based on coat color, tooth wear (Stander 1997), and gum-line recession (Laundré *et al.* 2000). Body mass and linear measurements were recorded. Body mass (weight) was recorded using a portable scale. All captured animals were released after their examination.

We contrasted the body mass ratio between species and sexes. For this we used the formula, (M-F)/[(M+F)/2]; where M is the average body mass of the males, and F is the average body mass of the females. This formula provides the difference in mass relative to the average mass of the sexes. In the case of the comparisons between different species of the same sex, we treat the species with the greater body mass (jaguars) as males (M), and the species with lesser body mass (pumas) as females (F).

We analyzed body mass, body length (head + body), tail length, head length, and shoulder height. We used the cube root of the body mass because the other measures are linear, while body mass refers to volume. Additionally, we used the length of the superior canines, distance between superior canines, distance between inferior canines, diameter of superior canines, and diameter of inferior canines. All measurements were log-transformed to improve normality, and all transformed variables were included in the analyses. We conducted a Principal Component Analysis (PCA) to evaluate and visualize variability in size between species and sexes, and to characterize groups of individuals according to these morphological variables. We performed the PCA using the function "prcomp" available in STATS package of R 3. 1. 1 (R Core Team 2016).

Because our sample size was small, we compared morphological variables using a one-way analysis of variance (ANOVA) to assess the significant differences between species and sexes. We used the species and sexes arranged in four different groups (male jaguar, female jaguar, male

Table 1. Mean and standard errors of body mass, body measurements and craniodental measurements of jaguars and pumas of southern Mexico. Body mass is in kg, all other measurements are in centimetres.

	Panthera onca		***Puma concolor***	
	Male (*n* = 2)	**Female (*n* = 3)**	**Male (*n* = 8)**	**Female (*n* = 3)**
Body mass	52.50 ± 3.53	34.33 ± 1.52	31.25 ± 5.23	21.33 ± 1.15
Body length	131.50 ± 3.50	118.33 ± 4.04	122.87 ± 5.89	108.66 ± 3.05
Tail length	53.00 ± 5.65	51.33 ± 4.16	63.00 ± 5.26	62.00 ± 3.00
Head length	32.00 ± 0.00	27.50 ± 0.86	25.75 ± 1.83	23.33 ± 0.57
Shoulder height	58.50 ± 0.70	51.00 ± 1.00	50.50 ± 2.67	46.00 ± 1.00
Superior canine length	3.45 ± 0.10	3.36 ± 0.17	2.49 ± 0.15	2.20 ± 0.08
Distance between superior canines	4.11 ± 0.20	3.65 ± 0.20	3.09 ± 0.14	2.83 ± 0.15
Distance between inferior canines	2.49 ± 0.01	2.43 ±0.18	1.92 ± 0.16	1.90 ± 0.14
Superior canine diameter	1.78 ± 0.04	1.49 ± 0.05	1.19 ± 0.07	1.08 ± 0.15
Inferior canine diameter	1.55 ± 0.09	1.43 ± 0.17	1.06 ± 0.09	0.79 ± 0.09

Table 2. Loadings for all variables for the first three principal components, and the variance explained, the cumulative variance explained and the standard deviation for the first three principal components.

	PC1	PC2	PC3
Body mass	-0.3409	0.2616	-0.1726
Head + body length	-0.2550	0.5368	-0.2930
Tail length	0.2296	0.5115	0.6202
Head length	-0.3400	0.1987	-0.1753
Shoulder height	-0.3270	0.3665	0.0111
Superior canine length	-0.3491	-0.1914	0.0431
Distance between superior canines	-0.3395	-0.1358	0.3515
Distance between inferior canines	-0.3013	-0.3548	-0.1589
Superior canine diameter	-0.3357	-0.1264	0.2457
Inferior canine diameter	-0.3208	-0.1052	0.5078
Proportion of variance explained	0.7349	0.1308	0.0525
Cumulative proportion	0.7349	0.8658	0.9183
Standard deviation	2.7110	1.1439	0.7246

puma and female puma) as explicative variables and the characters measured as response variables. If the ANOVA result was significant, we additionally implemented a pairwise comparison to determine significant differences between the groups for each character measured. We used a Bonferroni adjustment with the aim to control the Type I error across the pairwise tests. We assumed a significant α level of 0.05 for all tests. We performed the ANOVAs and pairwise comparisons using the functions "lm" and "pairwise.t.test" respectively available in STATS package of R 3. 1. 1 (R Core Team 2016).

Results

Five jaguars (2 males and 3 females) and 11 pumas (8 males and 3 females) were captured from November 2011 through April 2013 (Table 1). All individuals captured were classified as adults except for two male pumas which were juveniles. Using the average of body mass, male jaguar versus female jaguar ratio was 0.42, and in male puma versus female puma was 0.37. In the other hand, male jaguars were 0.50 times heavier than male pumas and female jaguars were 0.46 times heavier than female pumas. However, male puma versus female jaguar body mass ratio was –0.09, indicating that female jaguars are slightly heavier than male pumas in the southern Mexico.

The PCA analysis grouped the 16 measured individuals into four groups: male jaguars, female jaguars, male pumas, and female pumas, although with some overlap of the 95 % confidence intervals for male and female pumas (Figure 1). The first axis explained 73.5 % of the variance and grouped the male and female jaguars on the negative side of this axis by their body mass, head length, and superior canine length and diameter (Table 2). Meanwhile, male and female pumas remained on the positive side of the first axis, which means that jaguars are larger in these characteristics than pumas in southern Mexico. The second axis explained 13.1 % of the variance and grouped the individuals basically by their head + body length and shoulder height (with positive character loadings), and distance between inferior canines (negative loading). This axis represented size associated with body length and height, after the general size effect is removed. The positive side of the second axis included male jaguars and male pumas, and the negative side grouped the female jaguars and female pumas, which demonstrated that males of both species had relatively larger body lengths and heights than conspecific females, whereas females had relatively greater breadth between lower canines (Table 2, Figure 1).

With the ANOVA we detected significant differences between the species and sexes in all characters measured (for all characters, d. f. = 3, $n = 16$): body mass, F = 22.64, $P < 0.0001$; body length, F = 9.40, $P < 0.01$; tail length, F = 5.75, $P < 0.05$; head length, F = 15.26, $P < 0.001$; shoulder height, F = 13.83, $P < 0.001$; superior canine length, F = 44.43, $P < 0.0001$; distance between superior canines, F = 63.10, $P < 0.0001$; distance between inferior canines, F = 14.96, $P < 0.001$; diameter of superior canines, F = 33.62, $P < 0.0001$; and diameter of inferior canines, F = 19.97, $P < 0.0001$.

The pairwise comparisons revealed that jaguars were heavier than pumas, and that males of both species were heavier than females of the same species (Table 3). However, the pairwise comparison showed that body mass between female jaguars and male pumas were not significant different (Table 3). Furthermore, comparing all body measurements between female jaguars and male pumas, we detected significant differences in tail length only; male pumas had longer tails. These results indicate that female jaguars and male pumas were similar in body mass and size in southern Mexico (Table 1, Table 3).

However, we found a different pattern in the cranio-dental characters. Jaguars had longer canines, greater distances between both superior and inferior canines, and a greater

Table 3. Results (*P*-values) of the pairwise comparisons using the Bonferroni adjustment between jaguar and puma morphometric measurements in the Greater Lacandona Ecosystem, southern Mexico (body mass = BM; body length = BL; tail length = TL; head length = HL; shoulder height = SH; superior canine length = SCL; distance between superior canines = DBSC; distance between inferior canines = DBIC; superior canine diameters = SCD; inferior canine diameters = ICD).

Pair contrast	BM	BL	TL	HL	SH	SCL	DBSC	DBIC	SCD	ICD
Female jaguar vs. female puma	**0.0153**	0.2236	0.1140	**0.0268**	0.0840	**< 0.0001**	**< 0.0001**	**0.0036**	**0.0007**	**0.0003**
Male jaguar vs. female jaguar	**0.0029**	0.0873	1.0000	**0.0333**	**0.0137**	1.0000	**0.02444**	1.0000	**0.0233**	1.0000
Female jaguar vs. male puma	1.0000	1.0000	**0.0230**	0.6152	1.0000	**< 0.0001**	**0.0004**	**0.0011**	**0.0007**	0.0073
Male jaguar vs. female puma	**< 0.0001**	**0.0020**	0.3800	**0.0001**	**0.0002**	**< 0.0001**	**< 0.0001**	**0.0099**	**< 0.0001**	**0.0002**
Male puma vs. female puma	**0.0268**	**0.0081**	1.0000	0.1866	0.0532	0.087	0.1227	1.000	0.6717	0.0543
Male jaguar vs. male puma	**0.0002**	0.3114	0.1333	**0.0009**	**0.0028**	**< 0.0001**	**< 0.0001**	**0.0048**	**< 0.0001**	**0.0027**

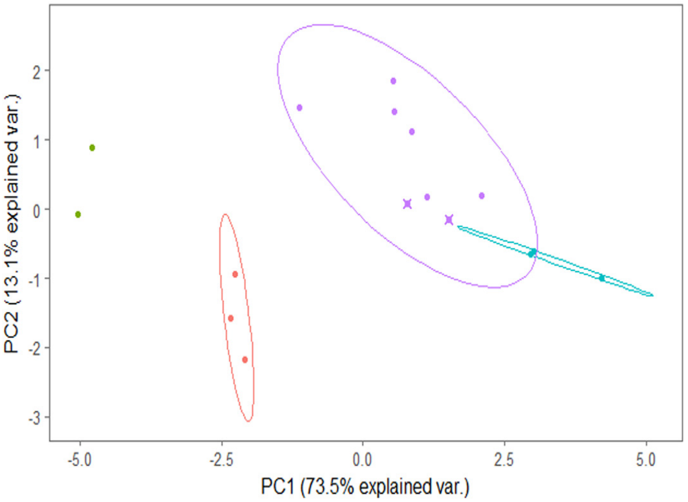

Figure 1. Principal Component Analysis of body and cranio-dental measurements. The first axis (PC1) accounts for 73.5 % of the total variation and, the second axis for 13.1 % of the total variation. See Table 2 for character loadings on these two components. Ellipses represent the 95 % confidence ellipses for each group (female jaguars, male pumas and female pumas). Green points represent male jaguars; red points female jaguars; purple points male pumas and turquoise points female pumas. The two juvenile pumas evaluated in this study include an "x" in the circle.

diameter in superior and inferior canines, than did pumas (Table 3). These differences between female jaguars and male pumas were significant for all cranio-dental characters (Table 3). Thus, although female jaguar and male pumas had similar body mass and size in southern Mexico, the size and robustness of canines and the mouth size were larger in female jaguars than in male pumas (Table 1, Table 3).

Discussion

Although sample size was small, we found significant differences in cranio-dental sizes between jaguars and pumas in southern Mexico. This finding suggests that character displacement between jaguars and pumas might be expressed not only by their body size, but also by their skull size, the length and robustness of canines, and breadth of the dental arcade. Caveats of this conclusion include that our sample size is small and that we did not include information of pumas from areas where this species is not sympatric with the jaguars. However, a larger cranio-dental size could confer an advantage to jaguars for hunting larger prey and for exploiting species that pumas are not able to use, although some overlap in body size between these two species may occur where they are sympatric (Emmons 1987; Taber *et al.* 1997).

Felid species show different morphological adaptations correlated with the size of prey taken (Meachen-Samuels and Van Valkenburgh 2009a, b; Sicuro and Oliveira 2011). Species that specialize in larger prey are distinguished by having a larger skull, more robust canines, a wider mouth, and a larger opening angle of the mouth. These characteristics are advantageous for dominating and killing large prey. On the other hand, felid species that specialize in taking small prey have smaller canines, a narrower mouth, a slightly longer jaw, and a greater bite force than the larger species relative to their body mass, and these features enhance their ability to capture small but agile prey (Christiansen 2007, 2008; Meachen-Samuels and Van Valkenburgh 2009a, b; Slater and Van Valkenburgh 2009; Sicuro and Oliveira 2011).

Generalist species, such as pumas, exhibit characteristics that are intermediate between these two groups, which indicates that they are adapted for taking prey of both sizes (Christiansen 2007; Meachen-Samuels and Van Valkenburgh 2009a, b). Additional evidence comes from the spectrum of prey taken in areas of sympatry. Pumas hunt a wider spectrum of prey than jaguars in areas of co-occurrence, and they often take smaller prey relative to jaguars (Rabinowitz and Nottingham 1986; Emmons 1987; Nuñez *et al.* 2000; Scognamillo *et al.* 2003; Novack *et al.* 2005).

Moreover, larger and more robust canines could enable jaguars to exploit other type of prey species that pumas are not able to use, or that they use with lower frequency than jaguars. For instance, it has been documented that due to the strength of their bite, jaguars can feed on vertebrates with hard skins or very resistant shells, such as crocodiles, turtles or armadillos (Rabinowitz and Nottingham 1986; Emmons 1989; Nuñez *et al.* 2000; Da Silveira *et al.* 2010; Arroyo-Arce and Salom-Pérez 2015; Guilder *et al.* 2015), and the occurrence of this kind of species in jaguar diet is greater than in pumas (Emmons 1987; Taber *et al.* 1997; Nuñez *et al.* 2000; Scognamillo *et al.* 2003; Foster *et al.* 2010).

It is important to consider that two of the male pumas evaluated in this study were classified as juveniles by their body and dentition condition. This probably could affect our results because the group that presented more variability in the body characters measured was the male pumas (Table 1). Nevertheless, cranio-dental characters in male pumas exhibited variability similar to that of the other three groups (male jaguars, female jaguars, and female pumas). This sug-

Table 4. Mean ratios of body mass between sexes (males M, females F) and species throughout the sympatric distribution of jaguars (J) and pumas (P).

Study area	Latitude	Sample size		FJ vs MJ	FP vs MP	FJ vs FP	MJ vs MP	FJ vs MP	MJ vs FP
		Jaguars	Pumas						
Jalisco, Mexico[a]	19° N	2 ♂; 4 ♀	3 ♂	0.51			0.21	0.31	
Lacandona Forest, Mexico[b]	16° N	2 ♂; 3 ♀	8 ♂; 2 ♀	0.42	0.37	0.46	0.50	-0.09	0.84
Los Llanos, Venezuela[c]	8° N	3 ♂; 2 ♀	2 ♂; 4 ♀	0.58	0.67	0.62	0.53	0.05	1.10
Emmas, Brazil[d]	- 18° S	2 ♂	3 ♂; 4 ♀		0.54		0.48		0.96
El Chaco, Paraguay[e]	- 21° S	13 ♂; 9 ♀	6 ♂; 2 ♀	0.30	0.55	0.79	0.57	-0.28	1.03
Mean				0.45	0.53	0.62	0.46	0.00	0.98
Standard deviation				0.12	0.12	0.17	0.14	0.24	0.11

[a]Nuñez, 2006, [b]This study.[c]Scognamillo et al., 2003, [d]Silveira, 2004, [e]McBride, 2009

gests that the effect of the juvenile individuals included in our analysis was reflected only in the body size variables.

By comparing the ratios of body mass between jaguars and pumas in sympatry, which were obtained from field projects carried throughout American continent, we observed that ratios of body mass between these species varied throughout their sympatric range (Table 4). Mean ratio in body mass between sexes of the same species ranged from 0.30 to 0.58 in jaguars and from 0.37 to 0.55 in pumas; between the same sex in jaguars and pumas the mean ratio in body mass ranged from 0.21 to 0.57 in males, and from 0.46 to 0.79 in females (Table 4). In general, male jaguars were larger than male pumas and female jaguars were larger than female pumas.

However, apparently female jaguars can have a smaller, similar or greater body mass than male pumas within their sympatric range (Table 4). For instance, female jaguars are smaller than male pumas in Jalisco, Mexico, have similar size to male pumas in southern Mexico and Los Llanos, Venezuela, and are larger than male pumas in the Chaco of Paraguay. The sample size of the studies analyzed was small, but this pattern probably is due because jaguars are smaller at the northern limit of their distribution range and their body mass increase towards South America. The variation in jaguar size seems is related with the availability of largest prey. Largest jaguars occur in the open floodplain habitats where they take largest prey, while smallest jaguars occur in forest habitats where they take smallest prey (Hoogesteijn and Mondlofi 1996; Sunquist and Sunquist 2009). This implies that female jaguars and male pumas could have similar body mass and size in much of their sympatric distribution, and that their cranio-dental differences have probably facilitated the resource partitioning and coexistence of these sympatric species that have substantially overlapping ecological requirements.

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References

Aranda, M., and V. Sánchez-Cordero. 1996. Prey spectra of jaguar (*Panthera onca*) and puma (*Puma concolor*) in tropical forests of Mexico. Studies of Neotropical Fauna and Enviroment 31:65–67.

Arroyo-Arce, S., and R. Salom-Pérez. 2015. Impact of jaguar *Panthera onca* (Carnivora: Felidae) predation on marine turtle populations in Tortuguero, Caribbean coast of Costa Rica. International Journal of Tropical Biology and Conservation 63:815–825.

Azevedo, F. C. C. de. 2008. Food habits and livestock depredation of sympatric jaguars and pumas in the Iguacu National Park Area, South Brazil. Biotropica 40:494–500.

Brown Jr., W. L., and E. O.Wilson. 1956. Character displacement. Systematic Zoology 5:49–64.

Christiansen, P. E. R. 2008. Evolution of skull and mandible shape in cats (Carnivora: Felidae). PLoS One:e2807.

Christiansen, P. E. R. 2007. Canine morphology in the larger Felidae: implications for feeding ecology. Biological Journal of Linnean Society 91:573–592.

Da Silveira, R., E. E. Ramalho, J. B. Thorbjarnarson, and W. E. Magnusson. 2010. Depredation by jaguars on caimans and importance of reptiles in the diet of jaguar. Journal of Herpetology 44:418–424.

Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-tov. 1990. Feline canines: community-wide character displacement among the small cats of Israel. American Naturalist 136:39–60.

de la Torre, J. A., and R. A. Medellín. 2011. Jaguars *Panthera onca* in the Greater Lacandona Ecosystem, Chiapas, Mexico: population estimates and future prospects. Oryx 45:546–553.

de la Torre, J. A., J. M. Nuñez, and R. A. Medellín. 2017. Spatial requirements of jaguars and puma in Southern Mexico. Mammalian Biology 84:52-60.

Emmons, L. H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. Behavorial Ecology and Sociobiology 20:271–283.

Emmons, L. H. 1989. Jaguar predation on Chelonians. Journal of Herpetology 23:311–314.

Foster, R. J., B. J. Harmsen, B. Valdes, C. Pomilla, C. P. Doncaster. 2010. Food habits of sympatric jaguars and pumas across a gradient of human disturbance. Journal of Zoology 280:309–318.

Frank, L., D. Simpson, and R. Woodroffe. 2003. Foot snares: An effective method for capturing African lions. Wildlife Society Bulletin 31:309–314.

Guilder, J., B. Barca, S. Arroyo-Arce, R. Gramajo, R. Salom-Pérez. 2015. Jaguars (*Panthera onca*) increase kill utilization rates and share prey in response to seasonal fluctuations in nesting green turtle (*Chelonia mydas mydas*) abundance in Tortuguero National Park, Costa Rica. Mammalian Biology 80:65–72.

Halstead, T. D., K. H. Gruver, R. L. Phillips, and R. E. Johnson. 1995. Using telemetry equipment for monitoring traps and snares.

Pp. 121–123, *in* Twelfth Great plains wildlife damage control workshop proceedings (Masters, R. E., and J. G. Huggins, eds.). Noble Foundation. Ardmore, U. S. A.

Harmsen, B. J., R. J. Foster, S. C. Silver, L. E. T. Ostro, and C. P. Doncaster. 2009. Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a Neotropical forest. Journal of Mammalogy 90:612–620.

Hoogesteijn, R. and E. Mondlofi. 1996. Body mass and skull measurements in four jaguar populations and observations on their prey base. Bulletin of Florida Museum of Natural History 39:195–219.

Iriarte, J. A., W. L. Franklin, W. E. Johnson, and K. H. Redford. 1990. Biogeographic variation of food habits and body size of the american puma. Oecologia 85:185–190.

Jones, M. 1997. Character displacement in Australian dasyurid carnivores: size relationships and prey size patterns. Ecology 78:2569–2587.

Jorgeson, J., and K. H. Redford. 1993. Human and big cats as predators in the neotropics. Symposium of the Zoological Society of London 65:367–390.

Kiltie, R. A. 1984. Size ratios among sympatric neotropical cats. Oecologia 61:411–416.

Kiltie, R. A. 1988. Interspecific size regularities in tropical felid assemblages. Oecologia 76:97–105.

Laundré, J. W., L. Hernández, D. Streubel, K. Altendorf, and C. L. Gonzalez. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

Lê, S., J. Josse, and F. Husson. 2008. FactoMineR: An R package for multivariate analysis. Journal of Statistical Software 25:1–18.

McBride, R. 2009. Project jaguar-Final report. Technical report for Faro Moro Ecoresearch- Moises Bertoni- Paraguay Ministry of Enviroment (SEAM). Paraguay.

Meachen-Samuels, J., and B. Van Valkenburgh. 2009a. Craniodental indicators of prey size preference in the Felidae. Biological Journal of the Linnean Society 96:784–799.

Meachen-Samuels, J., and B. Van Valkenburgh. 2009b. Forelimb indicators of prey-size preference in the Felidae. Journal of Morphology 270:729–744.

Medellín, R. A. 1994. Mammals diversity and conservation in the Selva Lacandona, Chiapas, Mexico. Conservation Biology 8:780–799.

Morales, M. M., and N. P. Giannini. 2010. Morphofunctional patterns in Neotropical felids: species co-existence and historical assembly. Biological Journal of the Linnean Society 100:711–724.

Novack, A. J., M. B. Main, M. E. Sunquist, and R. F. Labisky. 2005. Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. Journal of Zoology 267:167–178.

Nuñez, R., B. Miller, and F. Lindzey. 2000. Food habits of jaguars and pumas in Jalisco, Mexico. Journal of Zoology 252:373–379.

Nuñez, R. 2006. Área de actividad, patrones de actividad y movimiento del jaguar (*Panthera onca*) y del puma (*Puma concolor*), en la Reserva de la Biosfera "Chamela-Cuixmala", Jalisco. Master Thesis. Universidad Nacional Autónoma de México. Mexico.

Pfennig, K. S., and D. W. Pfennig. 2009. Character displacement: ecological and reproductive responses to a common evolutionary problem. The Quarterly Review of Biology 84:253–276.

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rabinowitz, A. R., and B. G. Nottingham Jr. 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. Journal of Zoology 210:149–159.

Romero-Muñoz, A., L. Maffei, E. Cuéllar, and A. J. Noss. 2010. Temporal separation between jaguar and puma in the dry forests of southern Bolivia. Journal of Tropical Ecology 26:303-311.

Rosas-Rosas, O. C., L. C. Bender, and R. Valdez. 2008. Jaguar and puma predation on cattle calves in northeastern Sonora, Mexico. Rangelands Ecology and Management 61:554–560.

Scognamillo, D., I. E. Maxit, M. Sunquist, and J. Polisar. 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan Llanos. Journal of Zoology 259:269–279.

Seidensticker, J. 1976. On the ecological separation between tigers and leopards. Biotropica 8:225–234.

Sicuro, F. L., and L. F. B. Oliveira. 2011. Skull morphology and functionality of extant Felidae (Mammalia: Carnivora): a phylogenetic and evolutionary perspective. Zoological Journal of the Linnean Society 161:414–462.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Silveira, L. 2004. Ecologia comparada y conservção da onça pintada (*Panthera onca*) e onça parda (*Puma concolor*) no Cerrado e Pantanal. Ph D. Thesis. Universidade de Brasília. Brazil.

Slater, G. J., and B. Van Valkenburgh. 2009. Allometry and performance: the evolution of skull form and function in felids. Journal of Evolutionary Biology 22:2278–87.

Sollmann, R., M. M. Furtado, H. Hofer, A. T. A. Jácomo, N. M. Tôrres, L. Silveira. 2012. Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. Mammalian Biology - Zeitschrift für Säugetierkunde 77:41–46.

Stander, P. E. 1997. Field age determination of leopards by tooth wear. African Journal of Ecology 35:156–161.

Sunquist, M. E., and F. C. Sunquist. 2009. Family Felidae. Pp. 54-169, *in* Handbook of the Mammals of the World (Wilson, D. E., and R. A Mittermeier). Vol. 1, Carnivores. Lynx Edicions. Barcelona, Spain.

Taber, A. B., A. J. Novaro, N. Neris, and F. H. Colman. 1997. The food habits of sympatric jaguar and puma in the Paraguayan Chaco. Biotropica 29:204–213.

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