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BODY MASS AND SKULL MEASUREMENTS IN FOUR JAGUAR POPULATIONS AND OBSERVATIONS ON THEIR PREY BASE

Rafael Hoogesteijn[1] and Edgardo Mondolfi[2]

ABSTRACT

Body mass and nine skull measurements of two floodplain (Pantanal and Llanos) and two forest (Amazon and Central America) jaguar (*Panthera onca*) populations, were analyzed to compare them, relate their morphometric dimensions to preybase and latitude, and examine the relationship with their subspecies status. Analyzing data from males and females separately, jaguar at all sites differed significantly for most variables studied, with the exception of rostral breadth, maxillary teeth row length, and pterygoid fossa breadth for both sexes, and postorbital breadth for females, which were either not or only weakly significant. Individuals from the floodplain populations were consistently larger in almost all parameters than the samples from the forest sites. The difference is independent of the subspecific status. Comparisons among the biomass values of prey taken at each site were also consistently higher for floodplain populations. Jaguar skull size and body mass seem to be more related to biomass of prey taken than to latitudinal location. The differences found in these four populations and the high number of Central American subspecies suggest that a revision of subspecies validity is needed. The reduction in the subspecies number is not only important from a taxonomic point of view but also from an ecological and conservationist one. The increase of our understanding of the phylogenetic heritage and morphological and ecological variation within the species is a priority for conservation.

RESUMEN

Se comparó peso corporal y nueve medidas craneanas entre dos poblaciones de jaguar (*Panthera onca*) de sabanas inundables (Pantanal y Llanos) y dos poblaciones de jaguar de selva (Amazonas y América Central). Analizando machos y hembras por separado, los animales provenientes de los diferentes sitios estudiados difirieron significativamente en

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todas las variables estudiadas, con la excepción de ancho del rostrum, longitud de la serie dental superior (canino al PM3) y ancho de la fosa pterigoídea en ambos sexos; y ancho post-orbitario en las hembras. Los jaguares del Pantanal y Llanos fueron consistentemente más grandes que los jaguares de selva en casi todos los parámetros estudiados. Estas diferencias fueron independientes del status subespecífico. Las comparaciones de la biomasa de presas consumidas en cada sitio indicaron que la biomasa fue consistentemente mayor para las poblaciones de sabanas inundables. El tamaño corporal y del cráneo de jaguares parece estar más relacionado con la biomasa de presas capturadas que con la localización latitudinal. Las diferencias encontradas entre estas cuatro poblaciones y la gran cantidad de subespecies centroamericanas, sugiere la necesidad de revisar la validez de las categorías de subespecies.

INTRODUCTION

The jaguar (*Panthera onca)* is the largest felid of the Americas, presently occurring from Mexico to northern Argentina. The jaguar survives in many different types of habitats such as semiarid areas in Mexico, semideciduous and thorn forests in the Paraguayan Chaco, humid multistrata evergreen forest in the Amazon, and cloud forest in the Andean foothills. Except for anecdotes and notes on its natural history, little was known of its ecology and biology until 1970. Research conducted in the last three decades has revealed its great adaptability to different habitats and prey bases, in addition to great variations in body size between areas (summarized in Hoogesteijn and Mondolfi 1993a).

Our preliminary analyses (Hoogesteijn and Mondolfi 1993b) suggested that the floodplain populations (living in the Pantanal and Llanos) had greater body sizes (head and body length and tail length), body mass, and skull measurements (skull and width) than jaguars from other parts of Venezuela and Central America. In this study we examined a larger sample and compared the body mass and skull size of jaguars from two forest areas vs. jaguars from two floodplain areas, relating those dimensions to preybase and latitude.

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METHODS

Data Sources

Data on body mass and skull measurements of jaguars from the Llanos and the Guayana region of Venezuela were collected during 14 years of veterinary professional practice. Reliable Venezuelan sport hunters also cooperated by weighing and measuring jaguars killed because of persistent cattle killing. They also checked stomach contents and lent the skulls for measurements. Data on head, body, and tail length were available but not used in this study, because there is a high variation, depending upon who did the measurement and whether the measures were taken along the curves or "between pegs" (Almeida 1976). Body mass and skull measurements data were more reliable. Skull measurements were checked by other researchers to reduce error.

In this study, the total length of skull is the distance from the anterior edge of the premaxillar bone to the rear point of the occipital crest. Skull width is the maximum distance between the outer edges of the zygomatic arches. A skull index was obtained by adding the two previous measurements for each skull. Skulls with only one of these measurements (length or width) were deleted from the database. We included data from Almeida (unpubl. data), for some skulls where only the skull index was available. Condilobasal length was measured between the anterior edge of the premaxillar bone and the posterior edge of one of the occipital condyles. Length of the upper tooth row was measured between the anterior edge of the upper canine and the posterior edge of the upper carnassial. The maximal length of the carnassial crown was also measured. Rostral breadth was measured behind the canines. Infraorbital and postorbital breadths were measured at the narrowest points between and behind the orbits respectively, and the breadth of the pterygoid fossa was transversely measured at the mid point (see Fig. 1).

Published measurements were pooled with the above unpublished data and separated into four geographical areas. The sample titled Central America consisted of data from Mexico (Pocock 1939; Aranda 1992), Costa Rica (Pocock 1939; Goodwin 1946), Guatemala (Petén) and El Salvador (Pocock 1939), Belize (Rabinowitz 1986; Rabinowitz and Nottingham 1986), and the northern Colombia's Magdalena Valley (Pocock 1939). All these data were considered as one forest group. This area is inhabited by five different subspecies (*P. onca arizonensis*, *P. o. veraecrucis*, *P. o. hernandesii*, *P. o. goldmani*, *P. o. centralis*), following Nelson and Goldman (1933). Pocock

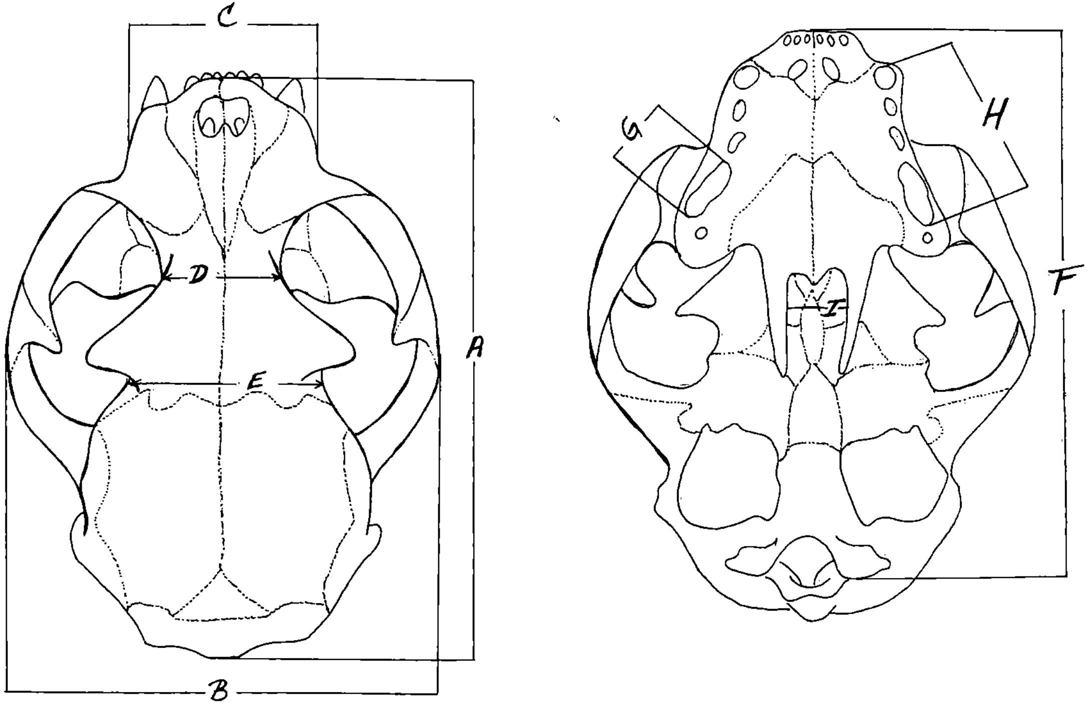

Figure 1. Measurements (in mm) of jaguars were taken as (A) skull length, (B) skull width, (C) rostral breadth, (D) interorbital breadth, (E) postorbital breadth, (F) condylobasal length, (G) upper carnassial tooth length, (H) upper maxillary tooth row length, and (I) pterygoid fossa breadth. (In the jaguar the last molar is placed medially to the PM3.)

(1939) and Seymour (1989) suggested that these five subspecies could be reduced to only one (*P. o. hernandesii*).

The second sample titled the Amazon block consists of animals from the subspecies *P. onca onca*, and from a second subspecies of dubious validity (*P. onca peruviana)* (Pocock 1939). These data are from Surinam (Pocock 1939; Husson 1978), from the Brazilian Amazon (Pocock 1939; Almeida, unpubl. data) and from the states of Bolívar and Amazonas in Venezuela's "Guayana region" (Pocock 1939; Hoogesteijn and Mondolfi, unpubl. data). All these data were considered as a second forest group.

The third sample consists of jaguars from the Llanos or floodplains of Venezuela (Hoogesteijn and Mondolfi 1993b, this study). The Llanos of Venezuela is a large, low lying savanna region that comprises much of the northern and western regions of the Orinoco River drainage basin in Venezuela and Colombia (Thorbjarnarson 1991). The jaguar population inhabiting this region is currently included in the same subspecies as the Amazon jaguar (*P. onca onca*).

Jaguars in the fourth sample come from the Pantanal or floodplains of southwestern Brazil and the bordering area of Paraguay and Bolivia. These data came from Allen (1916), Pocock (1939), Almeida (1976, unpubl. data), and Crawshaw and Quigley (1984). Measurements of some skulls from the Chaco of Argentina and Paraguay, and Rio Grande do Sul, Brazil, also were included in this group (Pocock 1939; Cabrera 1961; Ximenez and Silva 1979), since they belong to the same subspecies, *P. onca paraguensis*, (following Seymour 1989). The few skulls (5 males, 1 female) from the Chaco are smaller than those from the Pantanal, so the Pantanal skull size means are slightly reduced, rather than enlarged by the inclusion of these skulls. The data reported in the geographical areas included here, and their bibliographical sources are shown in Table 1.

The data in the literature that were not included are: (1) Some skull measurements of Mexican jaguars reported by Aranda (1992), and of Belizean jaguars reported by Rabinowitz and Nottingham (1986). These authors did not report the individual skull measurements, but only the means and standard deviations (S.D.) for males and females. These data are compared in the discussion section. (2) Two body mass measurements of very small Peruvian forest jaguars (both males in apparently good condition at 31 and 37 kg) taken by Emmons (1987), and some mass or skull measurements from localities that could not be clearly assigned to forest or floodplain areas of Perú and Bolivia (Pocock 1939) or Brazil (Crawshaw

Table 1. Site groups and references of jaguar mass and skull measurements utilized in the statistical analyses.

Forest Areas
- Site 1, Central America,
  - México (Aranda 1992; Pocock 1939)
  - Belize (Rabinowitz 1986; Rabinowitz & Nottingham 1986)
  - Costa Rica (Goodwin 1946; Pocock 1939)
  - Guatemala, Petén (Pocock 1939)
  - El Salvador (Pocock 1939)
  - Colombia, Magdalena Valley, (Pocock 1939)

- Site 2, Amazon Block,
  - Surinam (Husson 1978; Pocock 1939)
  - Brazil, Northern and Lower Amazon, (Pocock 1939; Almeida unpub.)
  - Venezuela, Guayana Region, (Pocock 1939; Hoogesteijn & Mondolfi 1993a, b; this study)

Floodplain Areas
- Site 3, The Llanos of Venezuela
  - Venezuela, States Apure, Guárico, Cojedes, Barinas, (Hoogesteijn & Mondolfi 1993a, b; this study)

- Site 4, The Pantanal
  - Brazil, Paraguay (Allen 1916; Pocock 1939; Almeida unpub.; Crawshaw & Quigley 1984)

  - The Chaco
    - Argentina, Paraguay, Southern Brazil (Pocock, 1939; Cabrera 1961; Ximenez & Silva 1979)

1992). (3) Data reported by Nelson and Goldman (1933), in their jaguar subspecies revision, since they are repeated in Pocock's (1939) work. (4) Following Pocock (1939), two skulls from Mexiana Island, Marajó, Brazil, since they only include the zygomatic width measurement.

A total of 128 body mass measurements, 156 skull lengths and widths, and 162 skull indices were included in the comparison of two forest samples (Central America and the Amazon) and two floodplain samples (the Llanos and the Pantanal) (see Tables 2-6). The number of skulls measured for the other variables are reported in Tables 7-9. A copy of the complete data set is available from the senior author.

To avoid the effects of age within and between samples (Fernandez and Lope 1994; Gay and Best 1996) subadults were eliminated from the analyses.

Data previously summarized by Oliveira (1992), in the form of the mean body mass of vertebrate prey index (MWVP), were used to compare the prey taken by jaguars in forest and floodplain areas. Only the results mentioned by this author were used, since we (and also Crawshaw 1995), found discrepancies between the results from the MWVP calculations obtained from the same data sets by different authors (Iriarte 1988; Oliveira 1992; Jorgenson and Redford 1993). This index is calculated as the geometrical mean obtained by summing the products of the numbers of individual prey times their $\log_e$ transformed mass, and divided by the total number of prey. An acknowledged shortcoming in comparing these studies is that the food habits were often quantified on the basis of unequal sampling efforts (sometimes with a small number of samples), in different seasons, or from different sources (feces, kills, or stomach contents), and it also depends on knowing prey size (adult or young prey), but such comparisons are useful to infer the differences among the areas included and their preybases. The inclusion or exclusion of domestic stock in the prey also was considered.

Statistical Analysis

Data of body mass in kilograms and skull length, width, index (length+width), condylobasal, carnassial, and maxillary teeth row length and the rostral, interorbital, postorbital, and pterygoid fossa breadth (all in millimeters) were analyzed by analyses of variance using SPSS # 6.0 and the SAS statistical package. Analyses were done separately for males and females to determine the site effect on each of the measurements previously mentioned. A separate analysis was done for the skull index including the site, sex, and sex x site interaction effects, with all the data of males and females combined. Differences between means were determined by Scheffe's multiple range test with a significance level of .05.

Table 2. Male jaguar mass (kg) by site.

Site	n	Mean	S.D.	Constant*
Llanos	26	104.5	±9.6	+12|
Pantanal	24	99.5	±11.2	+7|
Amazon	9	83.6	±9.7	-8
C. America	12	56.1	±5.7	-35
Total	71	92.0		92.0

* The constant represents the difference in means mass by site compared to the mean mass of all sites combined. Two groups with lines at the same level do not differ significantly.

RESULTS

Site Effect on Body Mass

Site effects for body mass (kg) were highly significant for males (f=76.49, $p<.001$). The Llanos group had the highest mean, followed by the Pantanal group. There were no significant differences between the two floodplain groups, but they differed significantly from the two forest groups, which also differed significantly from each other (Table 2). Site effects were also highly significant for females (f=42.82, $p<.001$). The Pantanal group of females had the highest mean, followed by the Llanos group and Central America. Amazon females were not included in the body mass analysis because of a small sample size. All three groups differed significantly from each other, the two floodplain groups were the heaviest (Table 3).

Site Effect on Skull Measurements

Site effects of skull length were highly significant in males and females (f=44.8, $p<.001$ and f=24.76, $p<.001$). For males, there were no significant differences between the two floodplain groups. Both had higher means and were significantly different from the two forest groups (Amazon and Central

Table 3. Female Jaguar mass (kg) by site.*

Site	n	Mean	S.D.	Constant
Pantanal	18	76.7	±9.0	+10
Llanos	31	66.9	±9.7	+1
C. America	8	41.4	±5.1	-25
Total	57	66.4		66.4

* Same observations as in Table 2. See text for comments.

America), which also differed between themselves, and had lower means. The number of observations and differences between means for males and females can be seen in Table 4. For females, the descending order was the same as in the males. The two extreme groups, Pantanal and Central America differ from the others, and the Llanos and the Amazon had no significant difference between them (Table 4).

Differences in skull width by site were highly significant in males and females (f= 41, $p<.001$ and f=15.85, $p<.001$ respectively). For males, there were no significant differences between the two floodplain groups (Pantanal and Llanos), which had the highest means, but they differed significantly from the two forest groups (Amazon and Central America), which did not differ between themselves (Table 5). For females, the descending order is the same as in males. The mean for the Pantanal females was higher and significantly different from the other groups. There was no significant difference for the mean of the Llanos and the Amazon. The Llanos differed significantly from Central America and the two lowest groups, Amazon and Central America, did not differ between themselves (Table 5).

Turning to the skull index, site effects were highly significant in males and females (f=52.91, $p<.001$ and f=22.81, $p<.001$). Statistical differences between the four male group means were the same as described for the males skull length (Table 6). The difference between the means of the female groups followed the same tendency as described previously for female skull width (Table 6).

Table 4. Male and female jaguar skull lengths (mm) by site*

Site	n	Mean	S.D.	Constant
Males				
Pantanal	48	290.5	±13.9	+09|
Llanos	23	289.6	±11.3	+08|
Amazon	19	262.6	±13.1	-19
Central Amer.	07	243.6	±07.9	-38
Total	97	281.4		281.4
Females				
Pantanal	28	257.6	±11.3	+10
Llanos	23	242.8	±09.3	-05|
Amazon	04	237.0	±10.9	-11|
Central Amer.	04	215.2	±12.3	-32
Total	59	247.6		247.6

* Same observations as in Table 2. See text for comments.

Table 5. Male and female jaguar skull widths (mm) by site.

Site	n	Mean	S.D.	Constant
Males				
Pantanal	48	194.2	±8.7	+06|
Llanos	23	194.1	±9.1	+05|
Amazon	19	175.9	±7.5	-13 |
Central Am.	07	166.4	±6.4	-22 |
Total	97	188.6		188.6
Females				
Pantanal	28	172.5	±6.5	+5
Llanos	23	166.1	±7.5	-1|
Amazon	04	160.2	±9.0	-7| |
Central Am.	04	148.7	±8.0	-19 |
Total	59	167.6		167.6

* Same observations as Table 2. See text for comments.

Table 6. Male and female jaguar skull indices (mm) by site.*

Site	n	Mean	S.D.	Constant
Males				
Pantanal	51	485.2	±20.7	+14 |
Llanos	23	483.7	±17.8	+13 |
Amazon	19	438.5	±19.5	-32
Central Amer.	07	410.0	±13.5	-61
Total	100	470.7		470.7
Females				
Pantanal	31	428.6	±6.5	+13
Llanos	23	408.9	±7.5	-06 |
Amazon	04	397.2	±9.0	-18 | |
Central Amer.	04	364.0	±8.0	-51 |
Total	62	415.1		415.1

* Same observations as Table 2. See text for comments.

Table 7. Male and female jaguar condylobasal lengths by site (mm)*.

Site	Male Means n = 72	Female Means n = 42
Pantanal	252.32 |	227.35 |
Llanos	251.30 |	219.98 | |
Amazon	235.31	209.90 |
Central America	223.14	194.70

* Same observations as Table 2. See text for comments.

Table 8. Male and female jaguar upper carnassial tooth lengths (mm) by site.*

Males (n = 73)			Females (n = 41)			
Site	Means		Site	Means		
Pantanal	29.25	│	Pantanal	27.69	│	
Llanos	28.26	│	Amazon	26.55	│	│
Amazon	28.06	│	Llanos	26.30	│	│
Central America	26.56		Central America	24.82		│

*Same observations as Table 2. See text for comments.

The differences in mean condylobasal length were highly significant for males and females (f=15.28, $p<.001$ and f=14.68, $p<.001$). The males followed exactly the same tendency as described for skull length. The number of observations and differences between means can be seen in Table 7. In females the descending order was the same as in the males, but there were no differences in the means between the Llanos and the Amazon females (Table 7).

Differences in upper carnassial tooth length by site, were highly significant for males and females (f=10.9, $p<.001$ and f=5.24, $p<.004$). The order of magnitude in the males was similar as described previously for the other skull measurements, but the only group that differed significantly from the others and had the smallest mean was the Central American one (Table 8). For the females the order of magnitude is slightly different, the group with the highest mean still was the Pantanal, but followed by the Amazon and the Llanos (which did not differ between themselves). The Central American group, also had the lowest mean, but it was not significantly different from the Llanos and Amazon means (Table 8).

In summary, mean skull length, width, index, condilobasal length in males and females and upper carnassial tooth length in males were highest in the floodplain groups and lowest in the forest populations.

Differences in interorbital breadth were surprisingly different. Site effects were significant for males (f=3.44, $p<.022$) and highly significant for females (f=12.79, $p<.001$). In males the order was Llanos, Central America, Pantanal, and Amazon, with no differences between the first three and the last three groups (Table 9), so the Central American group had the second largest mean in males. Central American females had the largest mean, statistically different from the other three groups, which did not differ between themselves (Table 9). This result, more consistent for the females, shows that despite having a smaller and narrower skull, Central American jaguars have a relatively broader frontal bone area at the interorbital breadth measurement point.

For upper maxillary tooth row length, rostral, pterygoid fossa, and postorbital breadth, site effects were not significant or only slightly so. Also the Scheffe's multiple range test was unable to detect significant differences between the group means.

Two-Way Interactions of Sex-by-Site

The complete data of skull indices of males and females were included and combined in an analysis including the effects of sex, site, and the two-way interaction of sex x site. All effects were highly significant, indicating that the relative differences between sexes were not the same in the different sites. The Pantanal and Central America groups have a difference of 30-31%

Table 9. Male and female jaguar interorbital breadths (mm) by site.*

Males (n = 68)		Females (n = 40)	
Site	Means	Site	Means
Llanos	55.92 |	Central America	57.39
Central America	54.73 | |	Llanos	48.26 |
Pantanal	52.15 | |	Pantanal	45.38 |
Amazon	49.07 |	Amazon	44.25 |

*Same observations as Table 2. See text for comments.

in body mass between males and females; the sex difference for the Llanos is 56%. Also the differences for skull measurements between males and females were greater for the Llanos (between 17 and 19%) compared with the other groups, where differences oscillated between 10% and 13%. There is apparently a higher degree of sexual dimorphism in the Llanos population than elsewhere (Table 10) .

Mean Mass of Vertebrate Prey Index

The values of the MWVP index are shown in Table 11. MWVP was lowest for forest jaguars. The first value was calculated from Aranda's (1992) work, with 18 fecal samples collected in Yucatán, México. The principal prey was collared peccary (*Tayassu tajacu*), coati (*Nasua nasua*), and red brocket deer (*Mazama americana*). These species constituted 83 percent of the total prey in this area, and had a MWVP value of 5.6 kg. The second MWVP value of 5.4 kg represents an average of two studies done in Belize (Rabinowitz and Nottingham 1986; Watt 1987). In one, 228 fecal samples were analyzed and the principal prey species were armadillo (*Dasypus novemcinctus*), paca (*Agouti paca*), collared anteater (*Tamandua mexicana*), and red brocket deer, species which constituted nearly 80 percent of the diet. In Watt's study 74 fecal samples were analyzed. The principal prey species were also armadillo, paca, small rodents, and collared peccary, species that constituted 60 percent of diet. This sample also included other smaller mammals and a larger proportion of iguanas and snakes. Watt's study was done in the same place but at a later date and, as suggested by this author, with a population of younger jaguars that were preying upon smaller species of prey.

The third MWVP value was calculated from data reported by Emmons (1987) from Cosha Cachu, Manú, Perú. Based on an analysis of 25 fecal samples, the MWVP value was 10.7 kg, which is larger than the two Central American sites. Principal prey consisted of large aquatic reptiles, large mammals such as collared peccary and brocket deer, large rodents (paca and agouti), and birds, all of which comprised 81 percent of the diet. The combined MWVP average for these three forested areas was 5.8 kg.

In comparison, MWVP for the floodplain jaguars was much higher. For two Brazilian studies, the MWVP only for natural prey (without cattle and sheep) was 32.4 kg. The first sample consisted of 59 kills from the Pantanal, Mato Grosso, Brazil (Crawshaw and Quigley 1984). The principal natural

Table 10. Morphometric differences in mass and skull dimensions between male and female jaguars (kg and mm).

	Differences											
	Mass			Skull Length			Skull Width			Skull Index		
Site	n	kg	%	n	mm	%	n	mm	%	n	mm	%
Pantanal	42	23	30	76	33	13	76	22	13	82	57	13
Llanos	57	38	56	46	47	19	46	28	17	46	75	18
Amazon				23	26	11	23	16	10	23	41	10
Central Am.	20	15	35	11	28	13	11	18	12	11	46	13

Each column has the number of males and females included in the analysis for each group, then the difference (in kg or mm) between males and females for the variable mentioned, and then, taking the female mean as 100%, the difference with the male in percentage is reported. See text for comments.

Table 11. Mean mass of vertebrate prey (MWVP, kg) for jaguar in forest and flood plain areas. * = with domestic stock, ** = without domestic stock.

Forest **	Mexico Feces		Belize Feces		Peru Feces		Total Forest Areas Average	
	n	MWVP	n	MWVP	n	MWVP	n	MWVP
	18	5.6	302	5.4	25	10.7	345	5.8
Floodplain *	Brazil Kills		Total Brazil Kills/StC[1]		Venezuela StC[1]		Floodplain Average	
	n	MWVP	n	MWVP	n	MWVP	n	MWVP
	59	113	80	70	18	50	145	89
Floodplain **	MWVP 34.3		MWVP 30.5		MWVP 32.4			

[1] = Stomach Contents
See text for comments

prey was capybara (*Hydrochaeris hydrochaeris*) and two peccary species. When cattle and sheep were included, the MWVP value for this study increased to 113.2 kg. The second Brazilian study was compiled from Schaller and Vasconcelos (1978), and Almeida (unpubl. data), using stomach contents and kills from the same region as the previous study. MWVP for natural prey was 30.5 kg, and when natural and introduced prey were included, the MWVP increased to 70 kg. Capybara, peccaries, feral hog (*Sus scrofa*), and caiman comprised 85 percent of the non-domestic prey taken. The average MWVP, including cattle, for the two Brazilian studies is 88.7 kg, a 15-fold increase compared with the preybase previously mentioned for the forest jaguars. A sample of six stomach contents from the Llanos of Venezuela gave an estimated MWVP of 98 kg, including domestic stock (Mondolfi and Hoogesteijn 1986). A larger sample (18 stomach contents) from the same area gave an MWVP value of 50 kg, where cattle remains occurred in 56 percent of the sample (Hoogesteijn and Mondolfi 1993a, b).

DISCUSSION

Means for body mass, skull length, skull width, and skull index reported in this study were higher than those previously obtained with a smaller sample (Hoogesteijn and Mondolfi 1993b), and are in the general range reported by other authors (Leopold 1959; Guggisberg 1975; Seymour 1989; Oliveira 1992). The mean values for Pantanal jaguars are in the same range as those reported before by Almeida (1976, unpubl. data). The means reported here also are in the same range as those given by Seymour (1989) for condylobasal length, zygomatic breadth, interorbital breadth, and length of upper carnassial in a sample of 112 skulls of males and females representing all subspecies.

The mean skull length of 243.6 ± 7.9 and 215.2 ± 12.3 mm and the mean skull width of 166.4 ± 6.4 and 148.7 ± 8 mm (both for males and females respectively) for Central American jaguars was fairly uniform compared to the same measurements reported by other authors for jaguars from the same area (males and females): 234.7 ± 5.79 and 213.8 ± 3.76 mm for skull length, and 161.2 ± 5.08 and 146.5 ± 3.26 for skull width for the Yucatán jaguar of México (*P. onca goldmani*) (Aranda 1992). This Central American subspecies is reportedly the smallest of all (Aranda 1992). Rabinowitz and Nottingham (1986) reported that skull length and width of jaguars in Belize (without stating subspecies, probably *P. onca goldmani*) measured for males and females (mean ± S.D. in mm) were respectively: length, 232 ± 26 (n=16 males), 216 ± 13 (n=3 females); width, 163 ± 8 (n=16 males), 150 ± 11 (n=5 females).

Important size variations in the jaguar have occurred since its arrival in America. Paleontological data suggest that jaguar "ancestors" were already present in the late Pliocene of North America, approximately 2-3 MYBP (million years before present). They also may have been part of the Holartic distribution of a large *Panthera* species. A jaguar related felid, *Panthera paleoonca*, was already present in Texas in the late Pliocene. It differed from the living jaguar in having longer carnassials (absolutely and relatively) and in having longer and more slender superior canines (Meade 1945). In the same area there is also evidence of a large felid (*Felis studeri*) that is related to the living puma. This latter species and the previously mentioned *Panthera* were nearly contemporaneous residents of the Texas Panhandle in the late Pliocene (Savage 1960).

In the Pleistocene's early Irvingtonian (1.5-1.9 MYBP), jaguars were abundant, while pumas were not, and where jaguar numbers and distribution shrank over time, puma numbers increased. During the Late Pleistocene (Late Blancan, ca 2 MYBP) pumas were only known from localities in southern North America. Pre-Wisconsinan jaguars (ca. 0.25 MYBP), on the other hand, ranged as far north as Washington, Nebraska, and Maryland. During the Wisconsinan, or last North American glaciation (less than 0.2 MYBP), the jaguar finds do not range as far north, reaching Nevada, Missouri, and Tennessee, and during the Late Pleistocene (less than 0.25 MYBP) the opposite occurred, pumas were found as far north as Idaho and Wyoming. More recently, jaguar records are concentrated in the southern parts of North America (Florida, Texas, and Tennessee), so the evidence indicates a gradual restriction of the jaguar's range in the Pleistocene-Holocene, although this general trend was probably influenced by a sequence of minor glacial-interglacial shifts. This reduction of the jaguar's range was followed by a reduction in body size. The Wisconsinan (ca 0.125 MYBP) jaguar (*P. onca augusta*) was 15-20% larger than its living counterpart. There is a progressive size reduction throughout this sequence in the Neartic, and this tendency is more pronounced in more recent times in the Holocene (less than 10,000 years ago), with specimens of intermediate size between Wisconsinan and living jaguars. Also there is a gradual shortening of the limbs, specially the metapodials, leading from a more generalized type to the characteristic jaguar form adapted to life in the forests, streams, and broken country (Kurten and Anderson 1980). Kurten (1965) stated that the large Pleistocene form probably was in direct genetic continuity with recent jaguars in areas where they still survive. Analyzing the size trends of the Pleistocene felids in Florida, he suggested that two important factors in short term oscillations are noted: (1) changes in the animal's adaptation to compensate for impoverished environment by size reduction (size could increase again under conditions of a favorable prey base); and (2) the adjustment to climatic and environmental changes. This latter factor gains probability when other data suggest an actual decrease in numbers, as in the case of the fossil jaguars of Florida (Kurten 1965; Kurten and Anderson 1980).

In South America, *Panthera* is definitely known from the Ensenadan onward (ca 0.4 to 1.5 MYBP) and Lujanian (ca 0.4 to 0.01 MYBP) in the late Pleistocene (Simpson 1970; Kurten 1973; Kurten and Anderson 1980; Anderson 1984; Seymour 1989). The jaguar and puma were already present in South America during the phases of contraction and expansion of savanna/forests areas in the Amazon region. Due to recurrent glaciations, growth of polar ice caps, sea currents, sea level regression, decreased rainfall, and increased fire frequency, the savanna/woodland expansion heightened approximately 18,000 YBP. Forested areas were reduced to island-like refugia and/or gallery forests along rivers and lagoons in areas where climate remained sufficiently humid to support forest biota. During that time, both felids and a large saber-toothed felid coexisted with an extremely large-sized assemblage of grazer and browser edentates and ungulates (e.g. megatheres, toxodons, glyptodonts, and haplomastodonts). This megaherbivore complex went extinct only some 8,000-10,000 YBP. With the new expansion of forested areas deriving from climatic shifts and a more humid climate, only the grazer/browser species more adaptable to savanna and forest conditions like *Tapirus*, *Hydrochoerus*, *Tayassu*, and *Dasypus* prevailed (Rancy 1991).

Today, the largest jaguars persist in the Pantanal of Mato Grosso (*P. onca paraguensis*) and the Llanos of Venezuela (*P. onca onca*), both floodplain areas (the Llanos nearer to the Equator) that are widely separated but possess some similar ecological features. Both are flooded 5-6 months of the year, covered in part with extensive gallery and semideciduous forests and have to a certain extent a similar preybase (Schaller and Crawshaw 1980; Crawshaw and Quigley 1991; Hoogesteijn and Mondolfi 1993a). Some questions arise regarding the size reduction that this felid underwent from the Pleistocene to the present and the actual large sizes of individuals from the two floodplain populations. These larger jaguars could represent descendants that maintained their larger size due to the better feeding conditions in the floodplain. On the other hand, local populations could have become bigger from the year 1,600 A.D. onwards, with the introduction of plentiful and vulnerable prey such as feral cattle, calves and horse foals. These prey constitute a sizable part of their diet; cattle constituted 38, 48 and 56% of stomach contents or kills in three studies, two in the Pantanal and one in the Llanos (Hoogesteijn and Mondolfi 1993b). These changes in size show the great adaptability of this efficient predator of the neotropical forest vertebrates. Most current studies relate jaguars to forested areas, but at the beginning of this century, with less human encroachment, jaguars still lived in open areas, like the Argentinean Pampas, where they sought cover in the high grass patches near lagoons and streams, areas practically devoid of forests (Canevari 1983). Also, jaguars lived in the lower Llanos areas where only small strips of gallery forests at the edge of rivers and temporary streams existed between enormous savanna expanses (Hoogesteijn and Mondolfi

1993b). In both places, due to the lack of extensive cover, they were easily exterminated.

It is possible that the jaguar as most of the other neotropical spotted cats, exhibits a certain intolerance to colder climates and their range waxed and waned with the recurrent glaciations. In the procyonids, Mugaas et al. (1993) have demonstrated that the raccoon (*Procyon lotor*) has the highest basal metabolic rate (associated with cold hardiness in mammals that live in cold-temperate and Arctic climates), the highest diversity of diet (associated with the ability to utilize a variety of food resources and to occupy a large number of different environments), and also a high intrinsic rate of natural increase. Other species of procyonids (e.g. *Bassariscus*, *Pottos)* showed intermediate or lower adaptation capacities, reflected in their more restricted distribution. The unique metabolic adaptations have given the raccoon the physiological flexibility to generalize its use of habitats and climates, and expand its geographic distribution to a greater extent than the other procyonids. The tendency in the felids is probably similar for the puma, adapted to both tropical and colder climates, and also with a high diet diversity along its extensive distribution (Iriarte et al. 1990).

The analyzed data show that floodplain jaguars (Pantanal and Llanos) have a larger body mass than the forest groups (Amazon and Central America), with no significant differences in the body mass of the males from the two floodplain groups. The same can be said for the statistically significant skull measurements (skull length, width, and index and condylobasal length in males and females; carnassial length in males), which also repeat the same tendency. The only exception was interorbital breadth, in which the Central American population had the second largest mean in males and the largest mean in the females. In the females, for the significant measurements, the order of magnitude is almost the same as in the males, but the Llanos female means for skull measurements were not significantly different than those from the Amazon in some of the variables studied. The group that is significantly smaller in all variables studied in both sexes (with the exception of the interorbital breadth) is the Central American, and the difference in mass within the group with the largest means is amazingly high. Llanos males have a mean body mass 50 kg heavier than Central American males (a difference of 86%). The females of the Pantanal weigh 35 kg more than the Central American females (85% difference). Crawshaw and Quigley (1991), also found that male jaguars in the Pantanal were approximately 80 percent heavier than males in Belize. This clearly relates to the prey base available for the floodplain and the forest populations, with the Central

American jaguars having the smallest prey base (MWVP 5.5 kg), the floodplain jaguars from the Llanos and the Pantanal the heaviest preybase (MWVP 89 kg), and the Amazon forest jaguars occupying an intermediate position (MWVP 11 kg). For the subtropical forest of Iguazu in southern Brazil, Crawshaw (1995) estimated a MWVP of 14.4 kg, a result also intermediate to the studies previously mentioned. The availability and vulnerability of prey are probably higher in the floodplain than in forested areas, important factors that influence prey selection by large felids (Sunquist and Sunquist 1989).

There appeared to be a high and positive relationship between MWVP values and body mass and skull measurements in the four populations studied. They were all higher in the floodplain sites and lower in the forest locations. Oliveira (1992), found a positive correlation between mean jaguar body mass and MWVP ($r=0.86$). Also, this author states that there is a strong correlation between body size and the usual mass of prey (MWVP), for a wide range of carnivore species. For the puma, MWVP values also were positively correlated ($r=0.83$) with body mass in all the different latitudes of America (Iriarte et al. 1990). McNab (1972) and Kiltie (1984) postulated that a correlation of body size with latitude in carnivores simply reflects the size of the available prey. The results from this study on jaguar body mass, skull measurements, and MWVP values, analyzed for forest and floodplain populations, clearly agree with McNab (1972) and Kiltie's (1984) conclusions. The results disagree with Rosenzweig's (1966) suggestions that it was "unlikely" that the size of the available prey was a factor responsible for variation in predator size. Iriarte et al. (1990) also state that puma prey selection, as well as body size, would be strongly influenced by size of available prey.

Data summarized by Oliveira (1992) from other authors show that in the Brazilian Pantanal, jaguar and puma have a degree of spatial separation and mutual avoidance, and although cattle is the main food for both species in the area, jaguars mainly prey on adults and pumas almost exclusively on calves. Also, the jaguar in tropical America has a higher MWVP (mean 49 kg) than the puma (mean 18 kg). In the Peruvian Amazon, these two species and ocelots preyed on different size classes: ocelots < 1 kg, puma 1-10 kg, jaguar > 10 kg (Emmons 1987). These findings and the fact that jaguars eventually kill pumas (Crawshaw and Quigley 1984) further support niche differentiation between these large felids. Body size is constrained by the presence of larger competitors (McNab 1972), and where these competitors are absent, a greater mean body size may evolve in response to various selective pressures. This argument is specially relevant to carnivore communities, because competing species generally fall along a gradient of body sizes (Rosenzweig 1966). For example, Nagorsen (1994) found that the greater body size of insular *Martes americana* in the Pacific Northwest is congruent with a lack of competitors on these islands, but the degree of size divergence is determined by prey size or abundance. Both jaguar and puma have smaller sizes and masses in areas of tropical forests, but the puma is generally smaller in areas where it is sympatric with the jaguar and increases in head-body size in areas outside of jaguar distribution, where it relies heavily on larger prey items than in tropical areas (Iriarte et al. 1990).

The jaguar is an opportunistic hunter that utilizes a great spectrum of prey species, more than 85 having been reported by Seymour (1989). Emmons (1987) suggested that its massive head structure is an adaptation to "cracking open" well-protected reptilian prey such as caimans, freshwater turtles, and tortoises, and documented predation on some chelonian species such as *Geochelone carbonaria* and *G. denticulata* (despite the shell's thickness and toughness), *Podocnemys unifilis* and *Platemys platycephala* (Emmons 1989). Other odd prey species mentioned by other researchers include the Orinoco dolphin (*Inia geoffrensis*) and saltwater chelonians (*Chelonia mydas*, *Lepidochelys olivacea*). The jaguar can subdue species potentially more dangerous or larger in size, such as crocodilians, giant-anteater (*Myrmecophaga tridactyla*), white-lipped peccary (*Tayassu pecari)*, and tapir (*Tapirus terrestris)*, species which the puma usually does not prey (Crawshaw and Quigley 1984; Hoogesteijn and Mondolfi 1993b; Carrillo et al. 1994). Further studies are needed to determine the ecological factors influencing jaguar and puma prey selection in areas of known prey availability.

The differences between the jaguar samples relate not only to body mass, skull sizes, or MWVP; there are also great differences in home range sizes. These differences are influenced by the type of habitat, the prey density, and the occurrence and degree of wet season flooding (Schaller and Crawshaw 1980; Rabinowitz and Nottingham 1986; Crawshaw and Quigley 1991; Crawshaw 1995).

A revision of *Panthera onca* is needed with regard to the validity of the present subspecies listing. A complete craniometric statistical study and DNA typing are needed. The results of this study highlight that the Llanos population is significantly different in body size and most of the skull measurements analyzed, compared to the Amazon jaguar, despite the fact that both are included in the same subspecies. The results also show little variation in the Central American group, suggesting that the five subspecies may in fact be a single subspecies.

Nelson and Goldman (1933) proposed a total of 16 jaguar subspecies, many based on one skin or one skull, or on skull characters used to describe subspecies that often varied within the same population. Pocock (1939) reduced the number of subspecies to eight, and he would have reduced them more if he had had complete access to the skull measurements used but not published by Nelson and Goldman (1933), who only gave measurements for some of the type skulls. Cabrera (1957) accepted Pocock's proposition to reduce the number of subspecies to three valid and one dubious one. Seymour (1989) suggested that, although Pocock did not have access to sufficient specimens in order to critically evaluate all the subspecies, his information implies that *P. onca goldmani* could be made into a synonym for *P. onca centralis*; *P. onca centralis*, *arizonensis*, and *veraecrucis* could be synonymous with *P. onca hernandesii*, and *P. onca peruviana* could be synonymous with *P. onca onca*. If these changes were made, there would remain only three subspecies *P. onca hernandesii*, *P. o. onca*, and *P. o. paraguensis*. For this last subspecies, Cabrera (1957) used the synonym *palustris*, which is based on a fossil, prompting Seymour (1989) to suggest that this synonym, following Nelson and Goldman (1933), should not be used in an extant subspecies. The reduction in the subspecies number is not only important from a taxonomic point of view but also from an ecological and conservationist one. The increase of our understanding of the phyllogenetical heritage, and morphological and ecological variation within the species is a priority for conservation.

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