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DO JAGUARS (*PANTHERA ONCA*) DEPEND ON LARGE PREY?

Carlos A. López González^{1,2} and Brian J. Miller¹

ABSTRACT.—The jaguar (*Panthera onca*) has been classified as an opportunistic hunter that takes as many as 85 prey species, according to availability. In this study we analyzed jaguar food habits throughout its range to quantify the importance of small, medium, and large prey in the diet. Because peccaries (*Tayassu*) are present in most studies, we also tested their importance in relation to other prey items. We conclude that jaguars are equally using medium- and large-size prey, with a trend toward use of larger prey as distance increases from the equator. There was no significant difference between the importance of peccaries and other large prey.

Key words: jaguar, *Panthera onca*, food habits, prey.

The jaguar (*Panthera onca*) is one of the least studied of the large felids, with most research carried out in the last 20 years (see review by Sunquist in press). Because jaguars are considered opportunistic predators, feeding on as many as 85 different prey items (Seymour 1989), it can be difficult to predict which prey species are regionally important, a point that is critical to conservation strategies.

In tropical areas where diets of jaguars have been studied, they generally eat medium- and large-sized mammals (Schaller and Vasconcelos 1978, Mondolfi and Hoogestijn 1986, Rabinowitz and Nottingham 1986, Emmons 1987, Aranda 1994, Crawshaw 1995, Aranda and Sanchez-Cordero 1996, Chinchilla 1997, Taber et al. 1997, Crawshaw and Quigley in press). In studies that analyzed more than 25 scats, 2 reported a preference for peccaries (*Tayassu pecari* and *T. tajacu*; Crawshaw 1995, Aranda and Sanchez-Cordero 1996), 2 reported preference for deer (*Mazama gouazoubira* and *Odocoileus virginianus*; Taber et al. 1997, Nunez et al. 2000), 1 reported preference for armadillo (*Dasypus novemcinctus*; Rabinowitz and Nottingham 1986), and 1 reported preference for reptiles (Emmons 1987). Four of these studies indicated use of large prey and 2 of those reported a dominant use of peccaries. Peccaries have a range that coincides with the jaguar, implying that those 2 species may have an evolutionary link (Aranda 1994).

In this study we analyze the value of large-, medium-, and small-sized prey to jaguars. We

also analyze peccaries both as part of the large prey category and separate from the other large prey to gain an understanding of possible evolutionary links.

METHODS

To test for preferences in jaguar diets, we reviewed dietary studies of jaguars in 10 different geographic sites ranging from 25 degrees South to 19 degrees North. Study sites included (north to south) Jalisco, Mexico (Nuñez et al. 2000), Campeche, Mexico (Aranda and Sanchez-Cordero 1996), Belize (Rabinowitz and Nottingham 1986), Costa Rica (Chinchilla 1997), Caatinga, Brazil (Olmos 1993), Peru (Emmons 1987), Peru (Kuroiwa and Ascorra in press), Paraguay (Taber et al. 1997), Argentina (Perovic in press), Iguazu, Brazil (Crawshaw 1995). A summary of the data used for the present analysis is presented in Table 1. Habitat type was obtained from the original publication, and when this description was absent we used the World Wildlife Fund classification. Human impact for each study site was classified as low, medium, or high based on the description in the original manuscript, and we included the status of the area as protected or not.

To standardize data and reduce bias associated with frequencies of occurrence (Ciucci et al. 1996), all data were converted to relative biomass consumed. Prey biomass consumed per scat produced was regressed against live body weight of the prey animals to determine

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TABLE 1. Database summary used to develop the present analysis.

Region (Latitude)	No. of scats	Habitat type	Human impact	Source
Jalisco (19°N)	47	Tropical dry forest	Low, protected area	Núñez et al. 2000
Campeche (18°N)	37	Tropical seasonal flooded forest	Low, protected area	Aranda and Sanchez-Cordero 1996
Belize (17°N)	228	Tropical rainforest	High, nonprotected area	Rabinowitz and Nottingham 1986
Costa Rica (8°N)	22	Tropical rainforest	Low, protected area	Chinchilla 1997
Peru—Cocha Cashu (8°S)	25	Tropical rainforest	Low, protected area	Emmons 1987
Peru—Madre de Dios (11°S)	13	Tropical flooded forest—riparian vegetation	Low, protected area	Kuroiwa and Ascorra in press
Brazil—Caatinga (11°S)	8	Tropical dry forest	Low, nonprotected area	Olmos 1993
Paraguay (20°S)	106	Tropical dry forest	Low to high, nonprotected area	Taber et al. 1997
Argentina (23°S)	246	Tropical dry forest	Low to high, nonprotected area, fragmented	Perovic in press
Brazil—Iguazu (25°S)	73	Tropical rainforest	High, protected area, fragmented	Crawshaw 1995

the relationship between body weight of prey and scats produced. The resulting linear relationship ($Y = 1.98 + 0.035X$; the letter Y indicates biomass of prey consumed per scat and X is prey body mass in kg) was then applied in the form of correction factor to convert frequency of occurrence values for each taxon to a relative estimate of biomass of each consumed (Floyd et al. 1978, Ackerman et al. 1984). The linear model used to convert frequency of occurrence to biomass consumed was developed for pumas (*Puma concolor*; Ackerman et al. 1984) and was applied to jaguars under the assumption of similar digestive tracts. A similar analysis has been applied to jaguars (Núñez et al. 2000), leopards (*P. pardus*), and tigers (*P. tigris*; Karanth and Sunquist 1995). Frequency of occurrence and percent occurrence typically overestimate the importance of small prey and underestimate the value of large prey in the diet (Ackerman et al. 1984, Karanth and Sunquist 1995, Núñez et al. 2000). Weights of most prey items were obtained from the respective studies; otherwise, we referred to Emmons (1997) and Reid (1997).

Prey were grouped into 3 categories: small (<1 kg), medium (1–10 kg), and large (>10 kg). In a 2nd analysis prey were grouped into 4 categories: small, medium, large excluding peccaries, and peccaries. Percent biomass for each prey category was arcsin transformed and compared for each study site and for data pooled across all study sites. These data were analyzed using a 1-way ANOVA, and significant differences were detected using Student-Neuman-Keuls multiple comparison tests (Zar

1984). Data from a given study site also were plotted against latitude to search for prey class patterns along a north–south gradient. $P > 0.05$ was considered nonsignificant.

RESULTS

Percent biomass consumed was similar between medium- and large-prey categories, with a very low proportion of prey use from the small category. A clinal pattern was evident from the comparison of prey and latitude. Jaguars living farther away from the equator used larger prey more frequently, whereas jaguars living nearer the equator depended more heavily on medium-sized prey (Fig. 1A).

Across all studies, average proportions of prey consumed by jaguars was $4.32 \pm 7.32\%$ for small-sized prey, $47.65 \pm 26.84\%$ for medium-sized prey, and $48.03 \pm 26.15\%$ for large-sized prey. Relative percent biomass differed among size classes ($F = 26.076$, $df = 2$, $P < 0.001$). Small-prey consumption was significantly different from consumption of medium-sized prey ($q = 8.905$, $P < 0.05$) and large prey ($q = 8.783$, $P < 0.05$). There was no difference in consumption of medium- and large-sized prey ($q = 0.122$, $P > 0.05$).

When peccaries were treated as a separate prey category from small-, medium-, and large-sized prey, percent biomass still differed among categories ($F = 10.435$, $df = 3$, $P < 0.001$). Although peccaries are present in most jaguar diets (mean biomass = $25.7 \pm 15.1\%$), their value to the jaguar diet is not significantly different from the rest of the large-sized prey

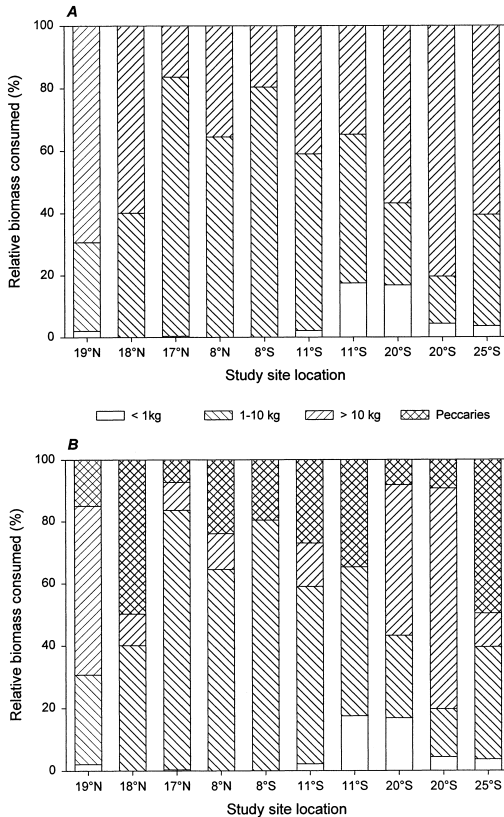


Fig. 1. North-south clinal variation in the percentage of biomass consumed by jaguars from prey categories. Data from Aranda and Sanchez 1996, Chinchilla 1997, Crawshaw 1995, Emmons 1987, Kuroiwa and Ascorra in press, Nunez et al. 2000, Olmos 1993, Perovic in press, Rabinowitz and Nottingham 1986, Taber et al. 1997. Graph A contains 3 categories: small, medium, and large prey. Graph B contains 4 categories: small, medium, large, and peccaries.

items ($q = 0.891$, $P > 0.05$; Fig. 1B). The use of small-sized prey by jaguars was different from medium-sized prey ($q = 7.862$, $P > 0.05$), large-sized prey ($q = 3.503$, $P < 0.05$), and peccaries ($q = 4.394$, $P < 0.05$). Use of peccaries was significantly different from use of medium-sized prey ($q = 3.469$, $P < 0.05$).

DISCUSSION

In our review of dietary studies, jaguars were not dependent on large prey and apparently can survive on medium-sized prey such as has been reported for leopards (Bothma and Le Riche 1986, Bailey 1993), cheetahs (*Acinonyx jubatus*; Laurenson 1995), and pumas

(Branch et al. 1996). Average mass of medium-sized prey was 4.0 ± 2.2 kg, which should be enough to maintain a large cat (considering the energetic model by Ackerman et al. 1986). Large prey, however, may play a more important role when females have kittens (see Ackerman et al. 1986).

In the studies we reviewed, researchers had no reliable way of determining which individual jaguar left a given scat, and this may have confounded analyses. Analyses may have been subject to pseudoreplication, with one individual contributing more heavily to results (see Hurlbert 1984). Ross et al. (1997) reported that food habits of solitary female cats can be significantly different from those of males.

Use of medium-sized prey by jaguars is also likely an artifact of human disturbance in a region. Unregulated harvest of large- and medium-sized prey by humans can significantly alter an ecosystem (Redford and Robinson 1987), and the disappearance of favored prey can force jaguars to prey upon livestock (Ackerman et al. 1986, Hoogesteijn et al. 1993). Prey declines also cause animals to move over greater distances, thereby increasing their vulnerability (Woodroffe and Ginsberg 1998).

We conclude that jaguars can use both medium- and large-sized prey that are available and behaviorally vulnerable (i.e., present in large groups, predictable distributions). We do not conclude, however, that either medium- or large-sized prey can be replaced adequately by the other category if prey in one category declines significantly.

From this review we could not conclude that peccaries, or any single prey species, were an important factor in jaguar evolution, largely due to the flexibility jaguars exhibit in prey acquisition (see Seymour 1989). In addition, humans have drastically altered the suite of available prey, making it difficult to draw evolutionary conclusions from recent information on prey selection.

Jaguar fossils exist in North America from the mid-Pleistocene about 1.5 million years ago (Seymour 1989, Turner 1997). During the mid-Pleistocene jaguars ranged over South and North America as far north as Washington, Nebraska, and Maryland, but in the Recent Epoch, the northern limit has been southern Arizona, New Mexico, and Texas (Seymour 1989, Brown and López González 2000). Because of this range reduction, Kurten and

Anderson (1980) stated that jaguars in their present range constitute a relict population of what was once a more widely distributed Holarctic form (see also Seymour 1989). Indeed, jaguar fossils in the north are older than those found in Central and South America, and North American fossils outnumber fossils of South America by 73 to 18 (Seymour 1989). Turner (1997) has proposed that the jaguar was likely driven from the more open habitat in the northern part of its range by the later appearance of the lion (*P. atrox*) in North America.

In contrast, the oldest peccary (*Tayassu*) records in the Americas are from the Late Pleistocene to early Recent (Mayer and Wetzel 1987), and the boundary between those 2 epochs was about 11,000 years ago. *Tayassu* probably underwent most of its evolution in Central and South America (Mayer and Wetzel 1987). Potential differences in time and centers of evolution would reduce the likelihood of co-evolution between peccaries and jaguars. It also indicates that although peccaries are certainly important jaguar prey, the range overlap between those 2 species may be correlated, but not causal.

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