Biogeographic variation of food habits and body size of the America puma

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Summary. The puma (*Felis concolor*) has the most extensive range of any terrestrial mammal in the Western Hemisphere, covering over 100° latitude. Food habits of different puma subspecies vary with latitude. Subspecies from temperate habitats generally eat larger prey and specialize on a smaller number of prey taxa, whereas, in tropical habitats, they prey on smaller, more varied prey. In North America, ungulates (primarily deer) represented 68% of the puma's diet by frequency of occurrence. Mean weight of vertebrate prey (MWVP) was positively correlated ($r = 0.875$) with puma body weight and inversely correlated ($r = -0.836$) with food niche breadth in all America. In general, MWVP was lower in areas closer to the Equator. Patterns of puma prey selection are probably influenced by prey availability and vulnerability, habitat characteristics, and potential competition from the jaguar (*Panthera onca*).

Key words: Puma – Jaguar – Food habits – Body size

There have been few studies on geographic variation of food habits within a single carnivore species (McNab 1971; Kurten 1973; Ralls and Harvey 1985; Bothma and Le Riche 1986). The puma (*Felis concolor*) is the largest member of its genus and has the most extensive range of any terrestrial mammal in America, covering over 100° latitude from the Strait of Magellan to the Canadian Yukon (Honacki et al. 1982). It is one of the most studied felids in America and food habits of several subspecies are well known (Anderson 1983). As might be expected from their distribution, puma subspecies show a great diversity in feeding ecology.

There are numerous studies on the trophic ecology of pumas in temperate (from British Columbia through California) and sub-tropical areas (Florida, Texas and northern Mexico) of North America, but few have been

done in the tropics of Central and South America (Currier 1983; Anderson 1983). Although this carnivore inhabits most of the Neotropics, its food habits and aspects of its feeding behavior have been studied only in central and southern regions of South America, such as the Pantanal region in southern Brazil (Schaller and Crawshaw 1980; Crawshaw and Quigley, unpublished work), southern Chile (Courtin et al. 1980), and the Chilean Patagonia (Wilson 1984; Yàñez et al. 1986; Iriarte et al., unpublished work).

The main goal of this study was to compare food habits of puma subspecies at different latitudes and to determine ecological patterns that might help explain puma prey selection.

Methods

Data Sources

We chose 15 studies from different sites in the Americas ranging from 51° north to 51° south. From the United States and Canada, we used studies from eight states or provinces (British Columbia, Oregon, Utah, Nevada, California, Arizona, New Mexico, and Florida; Table 1). We utilized two studies from Central America (Mexico and Belize), and six from South America (Pantanal in southern Brazil, Manu National Park in Peru, the northern Paraguayan Chaco, south-central Chile, and two studies from the Chilean Patagonia, Table 2). An acknowledged shortcoming of comparing such studies is that food habits were often quantified on the basis of unequal sampling efforts and sample sizes in different seasons and from different sources (stomachs, feces, direct observations, etc.). Sometimes we combined information from feces and stomachs or kills to calculate the percent of prey occurrence at each study site. Our analysis may be particularly sensitive to unequal samples from different seasons as puma food habits often exhibit yearly variation (e.g. Ackerman et al. 1984).

Statistical Analyses

We calculated the following parameters for each puma food habit study:
(1) Food niche breadth was determined by using Levins' (1968) formula:

$$B = 1/\Sigma\, p_i^2$$

where p_i is the relative occurrence (proportion) of prey taxon i in the diet. This index ranges from 1 to the number of categories used. We calculated food niche breadth at the species level for mammals and class level for other taxa. To enable us to compare populations of pumas with different numbers of prey categories (for instance, a larger number of prey categories produce a higher B value) we calculated standardized food niche breadth (B_{sta}) as proposed by Colwell and Futuyma (1971):

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

where B_{obs} is the observed niche breadth, B_{min} is the minimum niche breadth ($=1$), and B_{max} is the maximum possible niche breadth (the number of prey taxa taken by the predator in each study or site). B_{sta} ranges between 0 and 1. Neither niche breadth ($r = 0.24$, $F = 0.802$, d.f. $= 1$, $p = 0.39$) nor standardized food niche breadth was correlated with sample size ($r = 0.03$, $F = 0.013$, d.f. $= 1$, $p = 0.91$).

(2) The Mean Weight of Vertebrate Prey (MWVP) in puma diets was calculated as the geometric grand mean obtained by summing the products of the numbers of individual prey items with their natural-log-transformed weight and dividing by the total number of prey used in the calculation. Unless available, all individuals of a given prey species were assumed to be adult-sized. The MWVP index was used to determine the average body weight (biomass) of vertebrate prey eaten by pumas in each of the selected study sites. Mammalian prey species were divided into three major groups, based on their mean adult body weights: small = <1 kg, medium = from 1 to 15 kg, and large = >15 kg.

We compared MWVP with standardized food niche breadth (B_{sta}) and MWVP with average puma body weights (from Schaller and Crawshaw 1980; Anderson 1983; Roelke et al. 1986) across the range of latitudes encompassing the studied reports using SAS regression procedures (SAS Inst., Inc. 1988).

Results

Table 1 compares eight representative North American puma food habit studies. In all eight studies ungulates (especially deer) were the most frequent prey items, averaging 68% $\pm$ 20 ($\bar{x} \pm$ sd) of the total prey items in the puma's diet. Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces americana*), and porcupine (*Erethizon dorsatum*) were the most common prey items in these studies. A typical year-round study found deer composing 77% of the puma's winter diet and 64% of its summer diet by frequency of occurrence (Robinette et al. 1959). Large prey represented 78% $\pm$ 9 of puma's deit in North America.

The Florida puma subspecies (*F. c. coryi*) does not follow the North American pattern, having the highest food niche breadth and the smallest MWVP values (Table 1). White-tailed deer accounted for only 28% of the occurrence of prey in the puma feces, the lowest proportion of the diet for all the North American studies (Maehr et al. 1990). Although large prey accounted for over 70% of the total identified prey in puma feces, the abundance of feral hogs (*Sus scrofa*), raccoons (*Procyon lotor*), and armadillos (*Dasypus novemcinctus*) in the puma fecus resulted in a lower MWVP.

Anderson (1983) reported 31 puma food habit studies based on North American populations compared with only three from the Neotropics. The North American studies we examined tended to be more intensive than those in South American. Except for the studies

Table 1. Frequency of occurrence of major prey items in puma diets in British Columbia (BC) (Spalding and Lesowski 1971), Oregon (OR) (Toweill and Meslow 1977), Utah (UT) (Ackerman et al. 1984), Nevada and Utah (NE/UT) (Robinette et al. 1959), California (CA) (Dixon 1925), Arizona (AR) and New Mexico (NM) (Hibben 1937), and Florida (FL) (Maehr et al. 1990)

FOOD ITEMS	BC	OR	UT	NE/UT	CA	AR	NM	FL
TOT LARGE PREY	67.0	83.3	61.6	73.3	87.5	78.3	89.3	72.6
Deer	58.3	83.3	61.3	64.5	85.0	75.4	88.3	28.1
Livestock	8.7	0	0.3	8.8	2.5	2.9	1.0	44.5[a]
TOT MEDIUM PREY	26.2	16.7	20.4	20.7	2.5	20.7	8.2	25.2
Large Rodents	12.6	16.7	3.2	15.5	0	9.3	4.1	0
Carnivores	2.9	0	3.5	0.2	2.5	0	0.5	12.8
Lagomorphs	10.7	0	13.7	5.0	0	11.4	3.6	4.4
Armadillos	0	0	0	0	0	0	0	8.0
TOT SMALL PREY	0	0	10.1	3.8	0	0	0	2.2
Small Rodents	0	0	10.1	3.8	0	0	0	2.2
TOTAL MAMMALS	93.2	100.0	92.1	97.8	90.0	99.0	97.5	100.0
BIRDS	0	0	1.0	0	0	0	0	0
MISCELLANEOUS[b]	6.8	0	6.9	2.2	10.0	1.0	2.5	0
# Vert. Prey	103	18	316	486	40	330	200	75
# Feces	–	–	239	401	–	103	196	75
# Stomachs	103	18	–	277	40	15	–	–
Mean Body Weight	55.6	55.6	57.0	57.0	48.4	43.6	43.6	42.8
MWVP (kg)	47.1	47.8	42.3	41.0	43.0	41.0	39.8	17.1
Diet Breadth	1.6	1.4	2.4	2.2	1.4	1.7	1.3	3.6
B_{sta}[c]	0.15	0.19	0.21	0.20	0.12	0.17	0.06	0.37

[a] Includes wild hogs (*Sus scrofa*)
[b] Mainly carrion
[c] Standardized Diet Breadth

in southernmost Chile, the mean number of samples (feces and stomachs) per study examined in the Neotropics was 23 ± 20, eight times smaller than in North American (184 ± 124).

In contrast with North America, in Central and South America ungulates averaged only $35\% \pm 32$ of all prey items. Instead of large mammals, medium-sized and small ones such as capybara (*Hydrochaeris hydrochaeris*, average adult weight AAW = 28 kg, Eisenberg 1981), pudu (*Pudu pudu*, AAW = 8.5 kg, Courtain et al. 1980), and European hare (*Lepus capensis*, AAW = 3.4 kg, Iriarte 1988) made the most frequent contribution to the diet of South American pumas. Bird and reptile species, which rarely were recorded in North American puma diets (only 1% in Utah, Ackerman et al. 1984), represented more than 5% of the vertebrate items in puma diets in Central and South America (Table 2).

Small and medium-sized mammals from different taxonomic groups were important prey, with marsupials, lagomorphs, and large rodents being the most common. For example, in Brazil capybara represented 29% of the puma's diet (Crawshaw and Quigley, pers. commun.) and armadillos (*Dasypus spp.*) made up 32% of the pu-

ma's diet in the Paraguayan Chaco (Stallings, pers. commun.). In Central and South American tropical areas (Belize, Brazil, and Peru), the most important items were large and small rodents, averaging $25\% \pm 33$ of the items in the puma's diet.

MWVP in Central and South America ranged from 0.4 kg in Belize to 29 kg in Torres del Paine National Park (Table 2). The Pantanal MWVP value was not directly comparable because the data were based on kill-site analyses of large prey (mostly livestock) and not feces or stomachs (Crawshaw and Quigley, unpublished work). Studies in the temperate region of South America contrasted sharply with the tropical area studies. Chilean subspecies (*F. c. araucanus* and *F. c. patagonica*) had the lowest food niche breadths and the largest MWVP in South America (Table 2).

MWVP was inversely correlated ($r = -0.86$, $F = 32.2$, $d.f. = 1$, $p = 0.0001$) with standardized food niche breadth (B_{sta}) along the Americas (Fig. 1). The B_{sta} values from Central and South America were significantly greater than North America ($B_{sta} = 0.46$ versus $B_{sta} = 0.16$) (Florida was excluded because of its subtropical location and prey base; see discussion) ($t = 2.8$, $d.f. = 11$, $p = 0.03$; Ta-

Table 2. Frequency of occurrence of major prey items in puma diets in Central and South America. Data from: MacBride 1983 (Mexico); Rabinowitz & Nottingham 1986 (Belize); Emmons 1987 (Peru); Crawshaw and Quigley, unpubl. data (Brazil); Stallings, unpubl. data (Paraguay); Courtin et al. 1980 (Central Chile); Yáñez et al. 1986 and Iriarte et al. (unpublished work) (Southern Chile)

PREY ITEMS	MEXICO	BELIZE	PERU	BRAZIL	PARAGUAY	CHILE[1]	CHILE[2]
LARGE PREY	68.8	0	0	51.6	18.2	9.5	27.7
Deer	37.3	0	0	6.4	18.2	0	0.5
Camelids	0	0	0	0	0	0	17.1
Livestock	31.5	0	0	51.6	0	9.5	10.1
MEDIUM PREY	14.4	33.3	58.3	35.4	72.6	81.0	60.6
Pudus	0	0	0	0	0	81.0	0
Marsupials	1.5	33.3	0	0	0	0	0
Carnivores	12.9	0	0	0	4.5	0	6.6
Lagomorphs	0	0	0	0	9.1	0	54.0
Rodents	0	0	58.3	29.0	0	0	0
Peccaries	0	0	0	6.4	13.6	0	0
Armadillos	0	0	0	0	31.9	0	0
Anteaters	0	0	0	0	18.2	0	0
SMALL PREY	0	66.7	25.0	3.2	4.5	0	3.9
Monkeys	0	0	0	0	4.5	0	0
Rodents	0	66.7	16.7	0	0	0	3.9
Armadillos	0	0	0	3.2	0	0	0
Bats	0	0	8.3	0	0	0	0
TOT MAMMAL	83.2	100.0	83.3	96.8	100.0	90.5	92.2
BIRDS	16.8	0	0	3.2	0	9.5	7.4
REPTILES	0	0	16.7	0	0	0	0.1
Misc.[a]	0	0	0	0	0	0	0.3
# Vert. Prey	0	3	12	62	22	21	1182
# Feces	54	3	7	–	22	–	747
# Stomachs	–	–	–	–	–	–	–
# Kills	–	–	–	31	–	21	–
Mean Body Weight	43.6	35.0	28.0	31.0	35.4	32.2	55.6
MWVP (kg)	25.2	0.4	3.7	32.4	7.8	12.7	29.1
Diet Breadth	3.5	1.8	2.5	2.8	5.1	1.5	2.9
B_{sta}[b]	0.51	0.80	0.49	0.36	0.67	0.24	0.34

[a] Mainly carrion
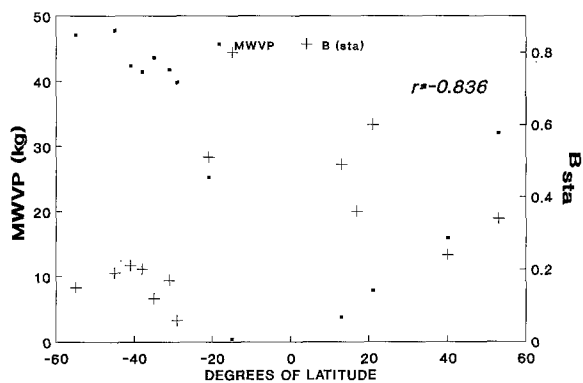[b] Standardized Diet Breadth

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Fig. 1. Relationship between mean weight of vertebrate prey (MWVP) and diet breadth of pumas along the Americas. Data from Tables 1 and 2
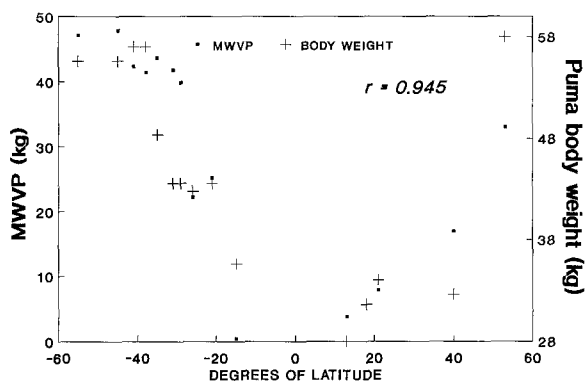

Fig. 2. Relationship between mean weight of vertebrate prey (MWVP) and body weights of pumas along the Americas. Data from Tables 1 and 2

bles 1 and 2). MWVP was positively correlated (r = 0.827, F = 27.07, d.f. = 1, p = 0.0003) with puma body weight at different latitudes (Fig. 2).

Discussion

The ability of the puma to adapt to such a wide range of habitats and prey makes it one of the most adaptable and generalist mammalian carnivores. Few other carnivore or mammalian species range from tropical and temperate rain forests to desert environs nor have such varied diets. Puma predatory habits must therefore depend on a wide range of geographically variable and often interrelated ecological conditions. This is reflected in the wide variety of different-sized species the puma prey upon throughout the Americas. In temperate North America pumas preyed extensively on large mammals, particularly deer, whereas in Central America, numerous different small and medium-sized species were utilized. In South America pumas preyed frequently on medium-sized items such as capybaras (Peru and Brazil), armadillos (Paraguay and Brazil), pudu (central Chile), and European hares (southern Chile). In the Patagonia of southern Chile, however, large prey (guanacos and sheep) made up a large proportion of the biomass consumed by pumas.

The specialization of North American puma on large prey, which represented 70% of their prey, was reflected by their lower than average food niche breadths. This contrasted with Torres del Paine National Park, in southern Chile, where large prey represented only 28% of the diet (combined data from Iriarte et al., unpublished work and Yáñez et al. 1986). Frequency of occurrence of medium-size prey (ranging from 1 to 15 kg) in Torres del Paine (Table 2) was over four times larger than the North American average (61% compared with 14%). This trend was especially evident with lagomorph species, which in North America represented less than 4% of all prey items, but in the Chilean Patagonia represented 54% of the occurrences in puma feces.

Two interrelated factors which influence prey selection in large felids are prey availability and vulnerability (Sunquist and Sunquist 1989). Although the puma is morphologically adapted to kill large prey, it may depend heavily on locally abundant small and medium-sized prey, especially when large prey are not available, or are less vulnerable. For example in southern Chile, pumas increased their predation on guanacos during the birthing season and period of juvenile expulsion, when this species was more vulnerable (Iriarte et al., unpublished work).

Predation in southern Chile was also related to prey abundance. The proportion of European hare in the puma's diet increased through the year as hare density increased through reproduction and was also greater in areas of high hare and low guanaco densities. Predation on guanacos has also increased as they have become more numerous in southern Chile. The proportion of guanaco remains in puma feces increased from 9 to almost 30% from 1982 to 1988, accompanied by an increase in the guanaco population from 670 to 1 300 during the same time period (Iriarte et al., unpublished work).

Similarly, in Florida, the frequency of deer remains in puma feces was greater in portions of its range with higher densities of white-tailed deer. Low deer densities in much of the puma's range in Florida may explain, in part, the low MWVP value of Florida pumas when compared with the rest of North America. Deer populations and densities of alternative prey species in portions of Florida may actually be critically low as pumas in areas of low deer densities are smaller, are in poorer condition, and have lower reproductive rates (Roelke et al. 1986; Roelke 1987; Maehr et al. 1989).

On the basis of these findings, we conclude the puma may forage selectively, with differences in predatory behavior throughout its range depending on local prey availability and vulnerability. There are additional factors, however, contributing to prey selection.

Puma subspecies in areas closer to the equator weigh less than subspecies at the extreme north and south of puma distribution. Similar patterns in puma size have been found based on skull measurements (Kurton 1973) and body-head lengths (McNab 1971). MWVP was positively correlated with puma body weight throughout the Americas (Fig. 2). This is consistent with the relationship between carnivore body size and their normal prey size

(Rosenzweig 1966; Schoener 1969; Gittleman 1985; Vezina 1985) and the hypothesis that the body size of American carnivores simply reflects the size of available prey (McNab 1971). Puma prey selection, as well as body size, would thus be strongly influenced by the size of available prey.

A closer examination of puma data across the Americas, however, demonstrates that size of available prey is probably not the only factor influencing puma size, but may also be related to the presence of sympatric carnivores. Even though prey larger that 15 kg are relatively abundant in tropical zones in Central and South America, pumas consumed almost exclusively small and medium-sized prey. For example, within the mammalian community of the Pantanal in southern Brazil the largest available prey species, the tapir (*Tapirus terrestris*, AAW = 150 kg), marsh deer (*Blastocerus dichotomus*, AAW = 80 kg), giant armadillo (*Priodontes maximus*, AAW = 55 kg), pampas deer (*Ozotoceros bezoarticus*, AAW = 40 kg), white-lipped peccary (*Tayassu pecari*, AAW = 28 kg), and cattle were preyed upon by pumas in low numbers (Schaller 1983). In Belize and Peru puma also preyed primarily on small to medium-sized prey in lieu of larger species available in the area (Rabinowitz and Nottingham 1986; Emmons 1987). Although these data are based on extremely small sample sizes and are not combined with either very accurate estimates of prey availability or an assessment of how prey biomass consumed relates to the number of field collectable feces, they do pose a question. Why does the puma, which relies heavily on large prey items whenever they are available in many parts of its range, appear to utilize them less in these tropical areas? One possibility is that characteristics of the habitat, perhaps its closed structure, are influencing prey selection by either making potential large prey less available (decreasing the probability of encounter), or by favoring the selection of smaller pumas more adapted to the terrain and thus better at exploiting smaller prey.

A second, but not exclusive, possibility is that puma prey selection is influenced by competition from the jaguar, which is the largest felid in America and sympatric with the pum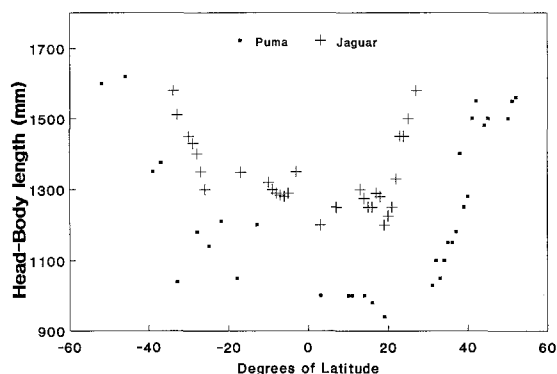a in most of its tropical distribution. Both the puma and jaguar have a similar relation between body size and distance from the equator (Fig. 3; McNab 1971), but the puma is generally smaller in areas where they are sympatric with the jaguar and increases in head-body size outside areas of jaguar distribution. Available data on puma and jaguar food habits in areas which they cohabit is too limited to accurately determine degree of dietary and habitat utilization overlap (Schaller and Crawshaw 1980; Rabinowitz and Nottingham 1986; Emmons 1987). However, jaguars could be important in determining resource partitioning and ultimately, body size of pumas in areas where they both are sympatric. Although character displacement has been found repeatedly in carnivores which are potential competitors (e.g. Seidensticker 1976; Bertram 1982; Dayan et al. 1990), it is still uncertain how similar species compete and community-wide character displacement occurs (King 1989; Pimm and Gittleman 1990).

Further study is needed to determine the ecological factors influencing puma prey selection. Concurrent studies of both the puma and jaguar in areas of known prey availability would be especially revealing.

Fig. 3. Puma and jaguar head-body length along the Americas. Data are from McNab (1971); Schaller and Vasconselos (1978); Anderson (1983); Currier (1983); Rabinowitz and Nottingham (1986); Mondolfi and Hoogesteijn (1986)

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