Food habits of jaguars and pumas in Jalisco, Mexico

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Abstract

Jaguars *(Panthera onca)* and pumas *(Puma concolor)* are sympatric over much of their geographic range in Mexico and South and Central America. We investigated diets of these felids in and around the Chamela-Cuixmala Biosphere Reserve in western Jalisco, Mexico. Diets were determined from scat analyses and documentation of prey cadavers. Relative biomass of each prey species consumed by pumas and jaguars was estimated from analysing 65 puma and 50 jaguar scats collected from 1995 to 1998. Both jaguars and pumas fed mainly on mammals, with white-tailed deer *(Odocoileus virginianus)* dominating the biomass of the diet of each species (54% and 66% respectively). There was a high degree of overlap between jaguar and puma diets, but pumas had a broader food niche than jaguars, and their ability to exploit smaller prey may give them an advantage over jaguars when faced with human-induced habitat changes.

Key words: *Panthera onca*, *Puma concolor*, diet, scat analysis, habitat, Mexico

INTRODUCTION

Jaguars *(Panthera onca)* and pumas *(Puma concolor),* the largest cats inhabiting the American continent, are locally sympatric over much of their range in Mexico and South and Central America. Coexistence of these similar species suggests they have evolved behavioural traits that ecologically separate them or that resources are abundant enough that sharing does not negatively affect either species. In either case, changes in habitat or prey abundance could alter the association between puma and jaguar, resulting in the decline of one or both species.

In tropical areas where diets of puma and jaguar have been studied, both species generally eat medium- and large-sized mammals (Schaller & Vasconselos, 1978; Mondolfi & Hoogestijn, 1986; Rabinowitz & Nottingham, 1986; Emmons, 1987; Iriarte *et al., 1990;* Aranda, 1993; Chinchilla, 1994; Crawshaw, 1995; Aranda & Sanchez-Cordero, 1996; Taber *et al., 1997;* Crawshaw & Quigley, in press). While pumas rely largely on deer *(Odocoileus* spp.) for more than 75% of their sustenance in temperate zones (e.g. Currier, 1983; Ackerman, Lindzey & Hemker, 1984; Logan *et al.,*

1996), their diet appears more varied in tropical regions (Dixon, 1982; Iriate *et al., 1990).*

There is a general lack of knowledge about predatory patterns of large cats living in the neotropics (Weber & Rabinowitz, 1996). There have been few field studies and results of studies that have been conducted vary among habitat types. Human impact has severely disrupted natural predator-prey assemblages in much of the world (Weber & Rabinowitz, 1996; Terborgh *et al.,* 1999).

It is likely that the predatory activities of large cats play an important rple in maintaining the biodiversity and structural integrity of tropical forest systems (Terborgh, 1990; Terborgh *et al.,* 1997; 1999; Miller & Rabinowitz, in press). Yet, habitat fragmentation, loss of prey and direct persecution are still reducing jaguar numbers in much of the Americas (Swank & Teer, 1989; Quigley & Crawshaw, 1992), and little is known about the status of tropical pumas. We analysed and compared the diet of jaguars and pumas on the Pacific coast of Jalisco, Mexico in an effort to understand better the interactions between large predators and prey in and around the Chamela-Cuixmala, Biosphere Reserve. Jaguars and pumas are the only two large carnivores in the area, and they are similar in body size, ranging between 30 and 50 kg in weight (Nufiez, Miller & Lindzey, in press).

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Study area

The Chamela-Cuixmala Biosphere Reserve (the Reserve) borders the Rio Cuixmala (19°25'N and 104°5'TW) on the coast of Jalisco, Mexico. The 130-km^2 reserve extends easterly from the Pacific Ocean, reaching an altitude of about 500 m above sea level. Terrain is rugged and hilly with arroyos separating the prominent hills. The 70 cm of annual precipitation fall between June and October, primarily during intense tropical storms and hurricanes (Bullock, 1986). Streams are ephemeral, and during the dry season free water is found only in scattered, isolated pools in the arroyos.

Nearly 90% of the Reserve's vegetation is classified as deciduous dry forest (Rzedowski, 1994; A. Miranda, unpub. data) with 95% of trees losing their leaves during the dry season. Trees of the dry forest are thickly distributed over the hills and are 10-15 m in height. Semi-deciduous medium forest, which typically maintains leaf cover during the dry season, occurs at lower elevations near the coast and extends along the arroyos into hilly inland areas (Gomez-Pompa, 1989). Trees of the medium forest are 15-25 m in height. In the 3000 km^2 area around the reserve, roughly 33% of the forest has been converted to agricultural purposes (A. Miranda, unpub. data). Human population growth and tourism development are expected to place additional demands on habitats and the wildlife they support.

METHODS

Scats were collected largely from the Reserve, but also from similar habitat in a 200 km^2 area bordering the Reserve to the north and east. Because of favourable soil conditions, we used tracks to determine the species of cat responsible for scats and prey cadavers (following Schaller & Crawshaw, 1980; Rabinowitz & Nottingham, 1986; Aranda, 1993, 1994; Aranda & Sanchez-Cordero, 1996). Scats or carcasses that could not be definitely assigned to either jaguar or puma were excluded from analyses. Scats were examined macro- and microscopically, and prey species found in scats were identified from hair and bone fragments by comparing them to reference hair and skeletal samples housed at the Estacion de Biologia, Chamela, IBUNAM (following Ackerman *et al.,* 1984; Emmons, 1987; Aranda, 1993; Karanth & Sunquist, 1995).

We calculated frequency of occurrence, percentage of occurrence and biomass of each prey species consumed (Ackerman *et al.,* 1984; Karanth & Sunquist, 1995; Taber *et al.,* 1997). Biomass calculations for jaguars and pumas involved a correction factor $(Y= 1.98 + 0.035 \, X)$ that was experimentally determined for pumas by Ackerman *et al.* (1984), where *Y* is weight of food consumed per scat and *X* is the total live prey weight. The larger surface area to body mass ratio of smaller animals means that bones and hair of smaller animals have a higher probability of being identified in

a scat. If percentage of occurrence of prey found in scats is uncorrected to biomass consumed, there will be a relative overestimate of small prey in the diet (Ackerman *et al.,* 1984). So, biomass consumed provides a more accurate representation of diet than either percentage of occurrence or frequency of occurrence (Ackerman *et al.,* 1984; Karanth & Sunquist, 1995). Because food habit studies are needed to predict the effect of predators on prey populations, accurate representation of the diet is important (Ackerman *et al.,* 1984).

The degree of dietary overlap between jaguars and pumas was calculated using the methods of Pianka (1973) and Morisita (1959 but modified by Horn, 1966). Breadth of diet was calculated 2 ways. The first method estimated prey taken in relation to the species of prey available locally (Levins, 1968), and the second method standardized the estimate to allow comparison among different regions (Colwell & Futuyma, 1971). Mean prey weight, calculated as a grand geometric mean, was estimated following Jaksic & Brakker (1983).

We estimated the sample size necessary to accurately depict diets of jaguars and pumas by assessing the point where additional scats did not change results. Initially, we calculated the percentage of occurrence of prey items in 10 randomly chosen jaguar and 10 randomly chosen puma scats. Calculations were then repeated adding groups of 5 more scats until all scats were included in analyses. The point at which additional samples did not change the results of analysis was estimated from accumulation curves (Korschgen, 1980) and observational area-curves (Mukherjee, Goyal & Chellum, 1994).

Diets of the 2 species were compared with G tests and equality of proportions tests (Zar, 1984). Level of significance was accepted at $P < 0.05$.

RESULTS

We collected 65 puma and 50 jaguar scats in and around the Reserve from 1995 to early 1998, with 84% of the scats collected during the dry season. Twenty other scats from large cats could not be classified to species. Carcasses of 19 animals killed by jaguars and 26 killed by pumas were found during the period.

Sample size

We estimated the number of scats necessary to adequately represent diet by analysing four dominant prey species for jaguars and five prey species for pumas. Using accumulation curves and analysis by G tests (Korschgen, 1980) we found that 35 and 40 scats were necessary to reflect the diet of jaguars and pumas, respectively. Asymptotes of area curves (Mukherjee *et al.,* 1994) indicated 40 scats adequately depicted the jaguar diet and 50 scats characterized the puma diet.

Table 1. Relative biomass of prey consumed by pumas based on 65 scats collected in the region of the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico, 1995-97

Category of prey	Frequency of occurrence	Prey weight (kg)	Correction factor	Relative biomass consumed	Percentage of occurrence
Odocoileus virginianus	55.38	30.0	3.3	66.09	37,11
Tayassu tajacu	10.77	10.0	2,4	9.19	7.22
Dasypus novemcinctus	13,85	6.0	2.2	10.96	9.28
Nasau narica	6.15	4.2	2.1	4.74	4,12
Ctenosaura pectinata	18,46	0.8	0.8	5.34	12.37
rodents	27.69	0.16	0.2	1,6	18.56
snakes	1,54	1,0	1,0	0.56	1,03
lizards	6,15	0.01	0.01	0.02	4.12
birds	3.08	0.02	0.02	0.02	2.06
Marmosa canescens	4.62	0.03	0.03	0.05	3.09
Didelphis virginiana	1,54	1,5	2.0	1,11	1,03

Table 2. Relative biomass of prey consumed by jaguars based on 50 scats collected in the region of the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico, 1995-97

Category of prey	Frequency of occurrence	Prey weight (kg)	Correction factor	Relative biomass consumed	Percentage of occurrence
Odocoileus virginian us	52	30.0	3.3	54.38	41,27
Tayassu tajacu	20	10.0	2.36	14.96	15.87
Dasypus novemcinctus	18	6.0	2.19	12,49	14.29
Nasua narica	22	4.2	2.13	14.85	17,46
Ctenosaura pectinata	8	0.8	0.8	2.03	6.35
Birds	4	0.02	0.02	0.03	3,17
Didelphis virginiana	2	1,5	2.0	1,27	1,59

Puma

Pumas killed 16 different prey species, 11 of which were found in scats (Table 1). Combined, puma scats contained 97 prey components (identifiable remains of an individual animal) for an average of 1,46 components per scat.. Vegetation was found in four scats, and two scats contained parts of plastic bags (there was a trash dump near the border of the Reserve).

Mammals composed 78% of occurrence in the puma diet and 94% of biomass consumed. Small mammals «< 1 kg) comprised 22% of occurrence and 2% of biomass consumed, medium-sized mammals (1-10 kg) comprised 14% of occurrence and 17% of biomass consumed, and large mammals (> 10 kg) comprised 42% of occurrence and 75% of biomass consumed. White-tailed deer, *Odocoileus virginianus,* alone, accounted for 66% of the biomass consumed in the puma's diet.. Reptiles represented roughly 18% of occurrence and 6% of biomass consumed.

In order of preference (via biomass consumed), the puma's five main prey species were white-tailed deer, armadillo *Dasypus novemcincus,* collared peccary *Tayassu pecari,* black iguana *Ctenosaura pectinata,* and coati *Nasua narica.* Combined, these species contributed 70% of occurrence and 96% of the biomass consumed by pumas (Table 1).

We found carcasses of 26 animals that had been killed by pumas. Those not identified in the scat analyses included domestic goat, bird *(Egreta thula),* mud turtle

Kinosternon integrum, unidentified fish and an ocelot *Leopardus pardalus.* The ocelot had been killed but not eaten.

Width of the puma's prey niche was 4.85 (following Levins, 1968), or 0.38 when standardized (following Colwell & Futuyuma, 1971). Average weight of prey species consumed by pumas was 12.7 kg.

Jaguar

Jaguars killed eight. different prey species, seven of which were identified in scats (Table 2). The 50 jaguar scats contained 63 cQmponents of prey for an average of 1.26 components per scat..

In the jaguar diet, mammals comprised 90.3% of occurrence and 98% of biomass consumed. Small mammals comprised 10% of occurrence and 2% of biomass consumed, medium-sized mammals comprised 33% pf occurrence and 29% of biomass consumed, and large mammals comprised 57% of occurrence and 69% of biomass consumed. The only reptile eaten by jaguars was the black iguana, representing 6% of occurrence and 2% of the biomass consumed.

In order of preference (via biomass consumed), the four main prey species of jaguars were white-tailed deer, collared peccary, coati and armadillo. Combined, these species contributed 89% of occurrence and 98% of the biomass consumed by jaguars (Table 2). White-tailed deer alone comprised 54% of biomass consumed by jaguars.

Table 3. Diet of jaguars in six locations: Calakmul Biosphere Reserve in Campeche, Mexico (Calakm); Chaco, Paraguay (Chaco); Cockscomb Reserve in Belize (Cocksco); Iguacu, Brazil (Iguacu); Cocha Cashew Research Station in Peru (Cashew); and Chamela-Cuixmala Biosphere Reserve in Jalisco, Mexico (CCBR). The number of seats (Seats (n)) and the number of species (Sp. (n)) identified is listed for each site. All data are reported in percentage of occurrence for consistency of comparison. All sites are between 16 and 19°N or 20 and 25°8. Chaco and CCBR are dry forests while the other four are wet or rainforest

		Calakm	Chaco	Cocksco	Iguacu	Cashew	CCBR
	Seats (n)	37	106	228	73	25	50
	Sp. (n)	10	23	17	17	40	7
Prey items:				Occurrence (%)			
peccary		42	5	5	36	15	16
deer		8	23	7	9	5	41
coati		18	–	1	6	–	17
armadillos		12	8	54	9	–	14
rabbits		–	23	–	1	–	–
small rodents		–	7	1	2	3	–
large rodents		4	–	14	6	15	–
reptiles		4	2	3	6	33	6

In addition to prey species identified in scat analyses, we found remains of a rabbit Sylvilagus cunicularis that had been killed by a jaguar. Width of the jaguar's prey niche was 3.97 (following Levins, 1968), or 0.50 when standardized (following Colwell & Futuyuma, 1971). Average weight of prey species consumed by jaguars was 15.6 kg.

Jaguars and pumas

Mammals dominated the diets of jaguars and pumas, with white-tailed deer providing over half the dietary biomass for both. We used the Morisita index (Horn, 1966), which compared biomass consumed, and the Pianka index (Pianka, 1973), which compared percentage of occurrence of prey species, to measure the dietary overlap between jaguars and pumas. Both methods indicated that jaguars and pumas had an extremely high degree of dietary overlap. The Morisita index was 0.96 (1.0 is complete overlap, 0 is complete separation), and the Pianka index was 0.84 (again 1.0 is complete overlap). While jaguars and pumas ate similar prey species, the proportion of prey species in their diets differed $(X^2 = 33.63$, G.L.=5, $P < 0.001$). Using an equality of proportions test, pumas ate significantly more rodents (largely cotton rats, Sigmoden mascotensis) than jaguars $(2_{0.05(2)} = 3.72$, $P < 0.001$), and jaguars ate significantly more coati than pumas $(2_{005(2)} = 2.77$, $P < 0.002$).

DISCUSSION

The relatively high mean weight of puma prey (12.74 kg) and jaguar prey (15.6 kg) indicated the importance of large animals in their diets, but despite a very high degree of dietary overlap between the two species, pumas had a broader prey niche than jaguars. Although our study indicated that white-tailed deer dominated the diet of both jaguars and pumas, other

species have been reported to be important in the neotropics. Table 3 and 4 present data from published studies in the neotropics that have used more than 25 scats to analyse the diet of jaguars (Rabinowitz & Nottingham, 1986; Emmons, 1987; Crawshaw, 1995; Aranda & Sanchez-Cordero, 1996; Taber et al., 1997; this study) and pumas (Taber et al., 1997; this study). In addition to the species listed in these studies, jaguars and pumas have been reported to kill primates (Chinchilla, 1994), capybaras Hydrochoerus hydrochaerris (Schaller & Vasconse10s, 1978; Crawshaw & Quigley, in press) and domestic animals (Mondolfi & Hoogesteijn, 1986; Rabinowitz, 1986; Quigley, 1987; de Almeida, 1990; Crawshaw & Quigley, in press).

These reports demonstrate the flexibility of jaguar and puma predatory patterns and indicate that they have enough behavioural plasticity to take advantage of a wide variety of prey species (Dixon, 1982; Currier, 1983; Rabinowitz & Nottingham, 1986; Emmons, 1987; Taber et al., 1997). Because choice of prey will be influenced by prey availability, abundance and vulner-

Table 4. Diet of pumas in two locations: Chaco, Paraguay (Chaco) and the Chamela-Cuixmala Biosphere Reserve in Jalsico, Mexico (CCBR). The number of seats (Seats (n)) and the number of species (Sp. (n)) identified is listed for each site. All dietary data are reported in percentage of occu/rr~nce for consistency of comparison to Table 3. Both sites are ry forest that are located 20°S and 19°N, respectively

	Chaco	CCBR
Seats (n)	95	65
Sp. (n)	16	11
Prey items:	Occurrence (%)	
peccary	9	7
deer	12	37
coati		4
armadillos	11	9
rabbits	9	
small rodents	16	19

ability (Emmons, 1987; Iriate *et al.,* 1990) it is not surprising that diets vary among regions.

We should be cautious about making evolutionary inferences from recent dietary data. The level to which human activity has eliminated species, changed habitat and disrupted predator-prey assemblages could have contributed greatly to the variability of diet reported in the literature.

In addition, dissimilar analysis techniques can make comparisons among studies problematic. For example, our analysis of diet reports both percentage of occurrence and biomass consumed, and the results support the prediction of Ackerman *et al.* (1984) and Karanth & Sunquist (1995) that using percentage of occurrence probably over-represents small prey and under-represents large prey. Dietary studies that analyse only carcasses and not scats, may overestimate the role of larger prey, as small prey are likely to be consumed entirely.

Comparisons are further complicated because some studies have reported results from low sample sizes (see reviews by Iriate *et al.,* 1990; Lópezz Gonzalez & Gonzalez Romero, 1998). We estimated 35-50 scats were necessary to document adequately diets of jaguars and pumas. When more potential prey species are available (e.g. in the humid tropics), a larger sample size of scats may be required.

To estimate numbers of individual animals consumed, we assumed that a jaguar and puma each need an average of 2-2.5 kg of meat a day (from Hornocker, 1970; Ackerman, Lindzey & Hemker, 1986; Emmons, 1987). This converts to 730-913 kg of meat per cat per year, although that quantity of meat will not be consumed in regular, daily 2-2.5 kg increments.

Based on our observations of carcasses in the field, we also assumed jaguar and puma returned to feed from deer or peccary carcasses 50% of the time. This rate of return is lower than that reported in puma studies from temperate regions, but carcass use can depend on rate of spoilage and abundance of prey (Ackerman *et al.,* 1986). After fasting for at least 1 day, Danvirs & Lindzey (1981) reported that captive pumas ate 6.8 kg of meat the first day and 3.5 kg the second day. Thus, assuming a 50% return the second day, jaguars and pumas would eat about 8.5 kg from each deer they killed. With 30% of a carcass being wastage (Hornocker, 1970; Ackerman *et al.,* 1986), peccaries (averaging 10 kg in weight) would be consumed entirely, as would smaller animals.

We converted data on biomass consumed into estimates of prey killed annually (following Ackerman *et al.,* 1984). Briefly, the estimate for the amount of meat eaten in a year (730-913 kg, see above) was multiplied by the percentage of biomass consumed for each prey species to provide kg of each prey species consumed. That amount was then divided by the weight of the prey item, if it was small enough to be consumed entirely, to give an estimate of the number of individuals killed annually. Deer were the only species too large to be entirely consumed and we estimated that jaguars and

pumas would eat 8.5 kg from each deer killed (see above).

By these calculations, a solitary jaguar may kill annually, c. 47-58 deer, 16-20 peccaries, 36-45 coatis, 22-27 armadillos and 19-23 black iguanas. A solitary puma may kill about 57-61 deer, 10-12 peccaries, 12-14 coatis, 19-24 armadillos and 49-61 black iguanas. At an estimated population density of 1.7 jaguars and 3.5 pumas per 100 km^2 in and around the reserve (Nufiez *et al.,* in press), the jaguar and puma populations may be killing 280-347 deer and 62-76 peccaries each year.

Mandujano (1992) used three techniques to estimate deer and peccary numbers in the Reserve, and reported a density of 12 deer and 7 peccaries per km^2. Thus, jaguars and pumas together are removing roughly 23-29% of the deer and 9-11 % of peccaries annually. These estimates compare favourably with several other studies. Pumas in Colorado (USA) take 12% of the deer population while human hunters take another 15% (Anderson, Bowden & Kattner, 1992), pumas in Arizona (USA) take 10-20% of the deer population (Shaw, 1980 in Anderson *et al.,* 1992), and pumas in Idaho (USA) take about 20% of the deer annually (Lópezz-Gonzalez, 1999).

The percentage of deer killed in and around the Reserve indicates that jaguars and pumas play a role in regulating deer numbers. Such top-down regulation by large cats in the tropics has been also reported by Terborgh *et al.* (1997). We therefore propose that if cats disappear from the general region there could be an over-abundance of deer in the Reserve (where they are protected). As an example of what this could portend, there is an over-abundance of white-tailed deer in National Parks of the eastern USA. This has resulted in the decline of some rodent species, the reduction of understory nesting birds, the decimation of the understory forest vegetation and the lack of canopy tree regeneration (McShea & Rappole, 1992; McShea, Underwood & Rappole, 1997).

Using our estimated densities of big cats (Nufiez *et al.* in press) and consumption rates per cat per year (see above), we predict a single jaguar or puma in western Jalisco feeds on about 38-48 kg of meat per km^2 per year. When jaguars and pumas are raising their young, however, the kittens are dependent for 16-19 months (Ackerman *et al.,* 1986), and an adult female providing for two kittens would probably need to double her intake of food (see Shaw, 1977; Ackerma~ *et al.,* 1986). These needs can be met by existing numQers of deer and peccaries in and around the Reserve, but they may also place jaguars and pumas in a vulnerable position if increasing human development reduces deer numbers in the region.

As humans colonize forested areas and alter the habitat, they also hunt large- and medium-sized mammals to supplement their diet (Redford & Robinson, 1987). A survey near the Reserve found the order of human hunting preference was deer, peccaries and armadillos, which mirrors the diets of jaguars and pumas. Decline in abundance of primary prey (in this

region, deer) will probably result in jaguars and pumas moving over larger areas to satisfy energetic needs, increasing contact with humans and therefore increasing human-induced mortality (see Woodroffe & Ginsberg, 1998).

The broader prey niche of the puma, and its ability to take smaller prey may give it an advantage over jaguars in human-altered landscapes. Indeed, 100 g-sized cotton rats, which are rarely found in natural forest, can reach densities of 19-900 kg per km^2 in areas that are cut and converted to land for cattle grazing (A. Miranda, unpub. data). In those disturbed areas they appeared in puma scats but were never found in jaguar scats. Jaguars rarely took any animal smaller than an armadillo, so habitat changes and decline of large prey may place more pressure on jaguars than pumas. In the long run, persistence of pumas appears more likely than jaguars in disturbed environments.

Additionally, if large prey decline, jaguars and pumas may select domestic livestock, which invariably follow human colonists, as an alternative food source (Hoogesteijn, Hoogesteijn & Mondolfi, 1993). If this happens, the level of conflict between humans and cats will escalate. Solutions to these conflicts are difficult.

CONCLUSION

Because large cats, and jaguars in particular, are sensitive to human activities, their presence in viable numbers can indicate a high level of regional, or landscape, ecosystem quality. At 130 km^2, the Chamela-Cuixmala Biosphere Reserve is too small to protect a viable population of jaguars and pumas by itself. If jaguars and pumas do not persist across the region, subsequent prey and mesopredator release could damage the biodiversity of protected areas such as the Chamela-Cuixmala Biosphere Reserve (e.g. over-abundance of deer inside the protected reserve could change the abundance and distribution of animals and plants). Put another way, the regional presence of jaguars and pumas may contribute more to ecosystem integrity inside of the Chamela-Cuixmala Biosphere Reserve than the Reserve contributes to viable numbers of jaguars and pumas in the region.

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